Patterns and Mechanisms of American Lobster (*Homarus americanus*)
Movement in the Northumberland Strait, Canada

by

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ABSTRACT

The Northumberland Strait, Canada, is a unique habitat in the southern Gulf of St. Lawrence (sGSL), which supports the only fall fishing season in the sGSL, established in part because of the belief that lobster migrate into the Strait. This thesis employs both Eulerian and Lagrangian methods to study the patterns and mechanisms of lobster movement in the Strait. In Chapter 2, an experimental trap survey documents a sequential increase in lobster catch from the north-west to the south-east, consistent with the observations of fishermen. While the increase in catch is largely a result of increased catchability associated with warm water, sequential increase along the axis of the Strait suggests immigration from the north-west. Both the change-in-ratio analysis and a trawl survey completed before and after the trap survey, indicate a three-fold increase in lobster abundance in the central part of the Strait in July. These results are remarkably consistent with trap catches in Shediac Bay 1932 and Egmont Bay 1981. Such a mass movement or migration may be associated with seasonal inshore/offshore migration, may be part of an ontogenetic shift or result from density-dependent dispersal. In Chapter 3, a mark/recapture tagging study found no directional bias in lobster movement during the summer, and the movement of lobster was consistent with a correlated random walk, such that the observed mass movement could result from diffusion along a gradient in lobster abundance, possibly associated with settlement hotspots. Further, female lobster had a higher mean displacement (13.89 km) than male lobster (10.89 km), which is consistent with female-biased dispersal associated with male territorial behaviour and female mate choice. In Chapter 4, I present the tracks of three resident lobster over three weeks. Of the eight lobster tagged with acoustic tags, the three lobster that stayed within the radio acoustic telemetry (RAPT) hydrophone array had a very limited home range (MCP < 1502 m^2) which is ideal for study with RAPT. The very different spatial scale of the movement documented in the second and third chapters demonstrates heterogeneity in American lobster movement behaviour in the Northumberland Strait. Research in other areas suggests that individual lobster are capable of a wide range of movement behaviour. However, if the heterogeneity of lobster movement documented here is associated with a mixing of populations with different movement behaviours, the intense fishery in the Northumberland Strait may undermine metapopulation structure.

LIST OF SYMBOLS USED

β	the angle of displacement between the direction of displacement between capture
χ^2	Chi squared
D	diffusion coefficient
n	the number of observation
N	number of tagged lobster reported
N_o	number of tagged lobster released
π	3.14
r	the mean vector
θ	the angle of displacement between the direction of between release and recapture
t	time, in days
x	displacement between release and recapture
c_{cj}	catch of canner- and sub-legal-size lobster during period j
c_{mj}	catch of market-size lobster
p_j	ratio of the catch comprised of canner- and sub-legal-size lobster during in a given sampling period (j)
p_o	ratio of the catch comprised of canner- and sub-legal-size lobster during the first time period
IR	immigration and recruitment rate
CL	carapace length

ACKNOWLEDGEMENTS

CHAPTER 1

Introduction

The abundance and distribution of organisms are central concepts in the study of population ecology (Andrewartha and Birch 1954). Linking abundance and distribution are movement, migration and dispersal. Understanding the patterns and mechanisms of movement, migration and dispersal is critical to the management and conservation of exploited populations. Dispersal defines populations (Dobzhansky and Wright 1943). It is inherent in population growth (Skellam 1951, Kot et al. 1996, Clark et al. 1999), can confer stability in the face of environmental change (Clark et al. 1999, Grosbois and Tavecchia 2003) and inhibit local adaptation (Olivieri et al. 1995). Even small-scale, within-population, movement creates population structure (Hanski 1999), such as that implicated in the collapse of Atlantic cod (*Gadus morhua*) (Hutchings 1996, Smedbol and Stephenson 2001, Beacham et al. 2002) and salmonid (Cooper and Mangel 1999) fisheries.

Dispersal, or lifetime net displacement, results from the accumulation of both small- and large-scale movements. Small-scale foraging (Kennedy 1961) or station-keeping (Dingle 1996) include movements associated with foraging, mate searching, predator avoidance and the exploration of and appropriation of nearby home ranges or territories. On a larger scale ontogenetic habitat shifts allow individuals to take advantage of more or different resources as they grow and mature. Here, I adopt Kennedy's (1961) definition of migration behaviour as "… persistent, straightened-out movement with some internal inhibition of the responses that will eventually arrest it." Migration behaviour may result in population migration or large-scale mass movements, such as those undertaken by insects, birds, fishes, butterflies, and free-ranging mammals, to make use of ephemeral habitats over a year, several years, and sometimes even over

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generations. Migration behaviour may also produce dispersal, which Turchin (1998) defines as "movement, which contributes to population spread." Dispersal can reduce the probability of inbreeding, competition among kin or form part of a bet-hedging strategy in temporally variable environments (Dingle 1996). From these definitions it follows, as Kennedy (1961) noted, that migration is directionally adaptive movement. I suggest that directionally arbitrary migration behaviour may be useful to distinguish between dispersal and migration.

A comprehensive research program on animal movement explores both population-level patterns and the mechanisms that produce the observed patterns (Herrnkind 1980, Turchin 2003). Identifying movement by changes in population distribution is referred to as a Eulerian approach, while tracking individual movement is called Lagrangian, after two mathematicians of the mid 1700's. Random walk, diffusion (Dobzhansky and Wright 1943, Skellam 1951, Turchin 1998) and competition (Murray 1967, Waser 1985, Buechner 1987) models bridge these approaches and predict population redistribution from individual displacement distances (Turchin 1998). However, in practice relatively few researchers attempt to link individual dispersal to population redistribution with diffusion models (Turchin 1998), as the basic assumptions of diffusion and competition models, homogeneous or quasi-homogeneous habitat and a population of identical individuals, are often violated.

Habitats are heterogeneous and movement behaviour is plastic. Plasticity in movement behaviour can be cued by heterogeneity in both the physical habitat and/or the biotic community. For example, conspecifics might attract or repulse individuals (Dingle 1996), and the presence of predators can modify prey behaviour, habitat preferences and

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even morphology (Childress and Herrnkind 2001, Gilliam and Fraser 2001). It is also rare that individuals within a population behave identically. Heterogeneity within populations or among individuals has been acknowledged in the literature by the recurrent use of arbitrary cut-offs based on dispersal distances to define rovers and sitters, dispersers and non-dispersers, and residents and transients for a range of taxa including insects (e.g. de Belle and Sokolowski 1987), fish (e.g. Beamish and MacFarlane 1987, Quinn and Brodeur 1991, Rodríguez 2002), birds (e.g. Verhulst et al. 1997), and mammals (e.g. Bunnell and Harestad 1983, Wiggett and Boag 1987). For some species, dispersal polymorphisms, such as presence or absence of wings in insects (Roff 1986), are easily identified, while for other species dispersal polymorphisms result from more subtle behavioural polymorphisms or syndromes (Fraser et al. 2001, Dingemanse et al. 2002). Reflecting differences in life history trade-offs, heterogeneity in movement or dispersal behaviours may also be associated with size, particular life-history stages or sex. Differential migration based on sex has been documented in several species of birds, humpback whales, and American eels (Dingle 1996). Partial migration, where only some individuals migrate, may also constitute a 'best of a bad job' where migration depends on state or condition (Kaitala et al. 1993, Dingle 1996).

The American lobster (*Homarus americanus*) fishery is both economically and socially important to the east coast of Canada. This research project arose out of concerns about a decline in lobster landings in the Lobster Fishing Area (LFA) 25, Northumberland Strait, Canada. While lobster landings have increased across the entire range of lobster since the mid to late 1980's, there has been spatial variability in the trends in landings (Fig. 1.3). Notably, LFA 25 landings increased earlier than other

fisheries in the southern Gulf of St. Lawrence (sGSL), thus raising the question of whether the decline in landings in LFA 25 is indicative of future landings in the rest of the sGSL.

Very little is known about the population structure of the American lobster, and attempts to use neutral genetic markers to identify population structure are undermined by a history of live transport for market, processing and scientific research as well as stocking in the early 1900's (Harding et al. 1997). Fishermen have long argued that there is a seasonal migration into the Northumberland Strait (Wilder 1963). Indeed, LFA 25 has the only late summer or fall fishing season in the southern Gulf of St. Lawrence (sGSL), in part established to accommodate the strongly held belief of fishermen that the lobster fishery in the strait depends on seasonal migration of lobster. However, tagging studies fail to show directed inshore/offshore movement (Templeman 1936, Wilder 1963, Comeau and Savoie 2002).

There are three lines of evidence, all of them based on population redistribution or a Eulerian approach, that support the claim that adolescent or adult lobster move into the Northumberland Strait in the summer: 1) changes in lobster abundance identified by bycatch in other fisheries or observation by commercial and recreational divers; 2) changes in the catch rates during the fishery; and 3) the size composition of the landed lobster. The first two arguments are largely supported by anecdotal evidence, although experimental scallop dragging prior to the opening of the scallop fishery in the Northumberland Strait found there to be very little bycatch of lobster in July in areas that supported a lobster fishery just weeks later (Jamieson and Campbell 1985). In support of the second argument, fishermen report catches declining at the end of the fishing season

sequentially from the east to the west. The third argument has been well documented (Lanteigne et al. 1998 and 2002). The greater proportion of larger market-size (≥81 mm CL) lobster in the landings in the Northumberland Strait suggests either that the lobster population is being supplemented by immigrants or that the population in the Northumberland Strait has a lower mortality rate than outside of the strait (Fig. 1.4). The largest source of mortality for adult lobster is the lobster fishery (Chadwick 1998), and it is probable that fishing effort and exploitation rate is greater in LFA 25 than other fishing areas in the sGSL as water temperatures are warmer during the late summer or fall fishery (Comeau et al. 2004) and rock crab (*Cancer irroratus*) bycatch in LFA 25 (Savoie 2002) may subsidize the lobster fishery.

The American lobster is a long-lived benthic invertebrate with a complex life cycle. While, it is generally accepted that for fish and decapods with complex life cycles dispersal occurs during the planktonic larval stages, recent studies of larval retention on coral reefs (Jones et al. 1999, Swearer et al. 1999) suggest that this assumption might warrant further investigation. Lobsters hatch into the water column, where they develop in the surface water for 6-8 weeks (Lawton and Lavalli 1995). Lobster larvae have limited swimming abilities, but settlement of postlarvae is selective for preformed crevices and macroalgae, and can be delayed for days if only sand substrate is available (reviewed by Ennis 1995). While the early benthic phases are cover seeking, adult lobster are more vagile.

Herrnkind (1980) categorized the movement patterns of spiny lobster as homing, nomadism, and migration:

"Migrations –the movement of an individual or a population over a considerable distance (vertical or horizontal), often periodically or with a return to the original area; nomadism –the wandering of individuals over a large area without clear-cut start and endpoints; and homing – the periodic, often daily, excursions from a shelter to some nearby area, with subsequent return to that shelter or others nearby."

These categories correspond roughly to migration, dispersal and foraging behaviours as defined by Kennedy (1961), however, under Herrnkind's framework dispersal movements could be described as migration or nomadism depending on the spatial scale. In the sGSL it takes 7-9 years for lobster to mature (50% maturity for females 70-72 mm CL, Lanteigne et al. 1998), and the maximum age of lobster has been estimated to be 70-100 years. The maximum recorded displacement of a tagged lobster was 798 km over 3.5 years (Campbell and Stasko 1986), although the majority of tagged lobster are recaptured less than 5 km from release sites (Comeau and Savoie 2002). For long-lived and highly mobile fish and decapods, like American lobster, the accumulated adult movements may be as important to lifetime net displacement as movement of larvae by currents.

Most of what we know of American lobster the distribution and abundance of adolescent and adult lobster is associated with commercial exploitation of lobster and other species. In addition to providing information on abundance and distribution through catch and bycatch data, lobster fishermen have been assisting in mark/recapture tagging studies for more than 100 years. While the minimum legal size for lobster varies among management units, the commercial fishery is generally limited to lobster at or above the size-at-maturity. In Canada, lobster fishing is also restricted to particular time periods for each of the management areas. Recognizing the biases associated with

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opportunistic fishery-dependent data, methods to directly observe lobster movement such as SCUBA, snorkelling and acoustic and electromagnetic telemetry, and to monitor changes in abundance, such as experimental trap and trawl surveys have also been employed. Particular approaches and methods are predisposed for the study of particular movement behaviours and patterns (Fig. 1.1). Here, I will review the literature on the patterns and mechanisms of lobster movement, paying particular attention to the methods for study.

Patterns of Movement or Population Redistribution

Seasonal Migration

The strongest evidence for the movement and migration of inshore lobster is inferred from changes in the distribution of lobster observed in commercial landings and experimental trap (Bergeron 1967; Munro and Therriault 1983; Moriyasu et al. 1998; Howell et al. 1999), SCUBA (Cooper et al. 1975; Ennis 1984) and trawl (Jeffries and Johnson 1974) surveys. As well, variations in the size composition of lobster catch, with more larger lobster inside than out, has been observed in the Magdalen Islands, Quebec (Bergeron 1967, Munro and Therriault 1983) and Malpeque Bay, Prince Edward Island (Moriyasu et al. 1998). On a smaller scale, direct observation by SCUBA diving and snorkelling has also documented a summertime increase in the abundance of lobster in shallow water in Newfoundland (Ennis 1984), Nova Scotia (Roddick and Miller 1992) and New England (Karnofsky et al. 1989a).

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Inshore/offshore seasonal movements have typically been described as a migration (Fig. 1.2a), with an assumed directed movement of lobster, but could also result from dispersal, spatially arbitrary migration behaviour (Fig. 1.2c). Directed migration into warm shallow water could confer fitness benefits associated with warmer water for moulting and mating (Bergeron 1967, Munro and Therriault 1983, Moriyasu et al. 1998). Inshore migration could also result form spatially arbitrary dispersal into seasonally available habitat (Jeffries and Johnson 1974, Howell et al. 1999, Watson et al. 1999). While, directed movement offshore may allow lobster to avoid low salinity in estuaries (Jury et al. 1994a, 1994b, Howell et al. 1999, Watson et al. 1999), increased wave action (Ennis 1984, Jeffries and Johnson 1974) and ice scour (Thomas and White 1968). Offshore movement may be of particular importance where over-wintering shelter is limited.

Partial Migration

Changes in sex ratio and size composition can also indicate differential mobility within a population. In both the Magdalen Islands, Quebec (Bergeron 1967, Munro and Therriault 1983) and an estuary in New England (Howell et al. 1999), the ratio of males to females varies spatially, with males predominating in the bay and females predominating in deeper water. Male-biased movement into estuaries may reflect the greater physiological tolerances of males and hence more available habitat (Jury et al. 1994a, 1994b, Howell et al. 1999, Watson et al. 1999). By contrast, females experience higher metabolic costs than males exposed to low salinity (Jury et al. 1994a) and tend to be more responsive to changes in salinity (Jury et al. 1994b). Similarly, a change in the

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ratio or proportion of injured lobster has been argued to indicate differential mobility in Malpeque Bay, Prince Edward Island (Moriyasu et al. 1998). While Moriyasu et al. (1998) suggest that the warmer water in the bay promoted growth and limb regeneration, Karnofsky et al. (1989a) proposed that the abundant transient lobster in the shallow bay were subordinates, and that dominant males were in deeper water, where females were more abundant there would be more opportunities for mating.

Ontogenetic Habitat Shift

Ontogenetic habitat shifts from shallow to deeper water are common for fish and decapods (review by Pittman and McAlpine 2005). Settling and shelter-restricted lobsters have narrowly defined habitat, while adult lobsters are found in a much greater range of habitat and at much greater depths (Lawton and Lavalli 1995). On the Atlantic coast, where surveys of settlement and juvenile lobster have been undertaken, settlement hotspots have been identified (Palma et al. 1999). Dispersal away from settlement hotspots may be density- or shelter-dependent (Steneck 2006) or be part of seasonal migration or dispersal.

Individual Movement Behaviour: Mechanisms of Population Redistribution

Station Keeping and Foraging Behaviour

Direct observation by snorkelling has been used to study small-scale foraging-type movement behaviour (Ennis 1984, Karnofsky et al. 1989a, 1989b). Ennis (1984) observed individual variability in lobster movement and residence-keeping, with

individuals alternating between nomadic and residence-keeping or homing behaviour. Karnofsky et al. (1989a, 1989b) tracked individual lobsters by snorkelling in a shallow bay. In their study (Karnofsky et al. 1989b) roughly half (52% of 334 lobster) the lobster were station keeping and associated with a particular area, den or series of dens. Karnofsky et al. (1989a) also showed that lobster can have affinity to home dens and may possess an intimate knowledge of their territories by returning to home dens after being transplanted within the bay, and suggested that some of the movement around the home dens was dedicated to maintaining knowledge of a temporally variable environment.

Owing to their large size, high mobility and exoskeleton, it is possible to attach electromagnetic and acoustic telemetry tags to lobster for continuous tracking (Jernakoff 1987, Jarvis 1989, Smith et al. 1998, Tremblay et al. 2003). Early studies using ultrasonic tags to track lobster (mean CL 78 mm) described two types of movement behaviour major (> 30 m) and minor (< 30 m), with a maximum daily rate of displacement at almost 2.5 km (Lund et al. 1970). Radio-acoustic positioning and telemetry (RAPT) is capable of high-resolution tracking but is limited to observing small-scale movements (Fig. 1.1). O'Dor and Webber (1991) report lobster movement of up to 3 km per day within a relatively well-defined home range. And, Tremblay et al. (2003) tracked movement of more than 500 m per day within a relatively well defined home range or area by ovigerous lobster in a shallow bay in Nova Scotia. The lobster in this study (Tremblay et al. 2003) were also more active at night than during the day. While the spatial and temporal scale of electromagnetic and ultrasonic telemetry studies has been limited by the expense of the hydrophone receiver arrays, more recently large-scale receiver arrays have been deployed (Bowlby 2006).

Migration Behaviour

The largest lobster displacement and the longest tracks recorded are from opportunistic mark/recapture tagging studies that depend on tag reporting by commercial fishermen. The lobster fishery is intense and animals released during a fishery may be recaptured in just a few days or may be re-caught years later (see review by Comeau and Savoie 2002). While opportunistic mark/recapture studies are cost-effective, the movement observed is biased by the spatial and temporal distribution of recapture (fishing) effort (Bumpus 1901 cited in Lawton and Lavalli 1995, Barrowclough 1978, van Noordwijk 1984, Porter and Dooley 1993, Hilborn 1990, Baker et al. 1995, Koenig et al. 1996, Whitehead 2001, Albanese et al. 2003). In Canada, the designation of lobster fishing seasons further biases mark/recapture tagging. For example, annual return migrations may not be detected if the release period immediately precedes or follows the fishing season.

Tracks established by multiple recaptures of tagged lobster or relocations by diving or acoustic tagging over days and weeks can describe large-scale migration behavior associated with seasonal migrations, ontogenetic habitat shifts and dispersal or namadism (Fig. 1.1b). Multiple recaptures of tagged ovigerous females have revealed seasonal onshore-offshore migration off of Nova Scotia (Campbell 1986, Pezzack and Duggan 1986). Unfortunately, multiple recaptures of this commercially valuable and intensely fished species are not abundantly available in inshore waters, and most mark-recapture studies report only single displacements. On the whole these net displacements show no clear directional bias, suggesting that the large-scale lobster movements are dispersal movements (Templeman 1936, Wilder 1963, Comeau and Savoie 2002).

Sex-Biased Movement

For American lobster, both male- and female-biased movement has been identified by tagging studies (Campbell 1986, Comeau and Savoie 2002). On the Atlantic coast, female-biased movement may be related to the maintenance of optimal temperatures for egg development (Campbell and Stasko 1986). While, the female-biased dispersal documented in 5/19 lobster tagging studies in the sGSL reviewed by Comeau and Savoie (2002) may be associated with greater mobility of mate-searching females relative to territory-defending males (Atema et al. 1979), in the same way that movement can be biased in some species of birds in which males establish nests (Greenwood 1980, Clarke et al. 1997).

Alternate Movement Behaviours

There is considerable evidence for within individual variability or plasticity in lobster movement. Ennis (1984) observed individual variability in lobster movement and residence-keeping, with individuals alternating between nomadic, migration behaviour, and station keeping, homing or foraging behaviour. He also documented a seasonal shift in activity with more resident of station keeping behaviour in the colder winter months. With a mobile hydrophone (e.g. Maynard and Conan 1984, Watson et al. 1999) it is possible to track lobster with acoustic tags over larger distances, but with less frequent observations (days or weeks). Watson et al. (1999) positioned lobster with acousitic tags roughly every three days for up to a year were found to alternate between directionally persistent movements and long periods (several weeks to months) with no detectable (within 0.1 km) movement.

Thesis Outline

The primary question addressed in this thesis is whether or not there is a migration of lobster into the Northumberland Strait. In this thesis, I use both Eulerian and Lagrangian approaches to document a pattern of adult and adolescent lobster (55-122 mm Carapace Length) movement and explore the mechanisms that produce the observed pattern. After presenting evidence for a mass movement or migration of lobster into the strait, I explore the mechanisms that would produce a mass movement of lobster into the strait, specifically I designed a mark/recapture tagging study to look for evidence of seasonally directed inshore/offshore movement. The warmer shallow water in the summer could enhance lobster growth, while a lack of suitable shelters and increased wave action in the fall and ice scour in the winter, may make the Northumberland Strait unsuitable. To avoid unfavorable conditions lobster may over-winter in shallow estuaries (Thomas and White 1969) or move to deeper water.

In Chapter 2, I report the results of an experimental trap survey designed to identify changes in abundance and distribution along a depth gradient and along the north-west to south-east axis of the strait. In Chapter 3, I report the results of an opportunistic individual mark/recapture tagging study. This survey was designed to identify directed movement associated with a seasonal inshore/offshore migration and provide data to test hypothesis about sex- and size-biased movement. Further, I use the mark/recapture data to test the hypothesis that individual lobster movement is density-dependent. And finally, I use a diffusion model to describe the density-distance distribution as an attempt to link the individual movement to the observed pattern of redistribution. In Chapter 4, I report the results of a pilot study using RAPT to describe

small-scale foraging behaviour and lobster activity in the Northumberland Strait. This data also provides an opportunity to identify diurnal activity patterns. And finally, in Chapter 5 I discuss the results of this thesis in the context of lobster ecology, management and conservation.
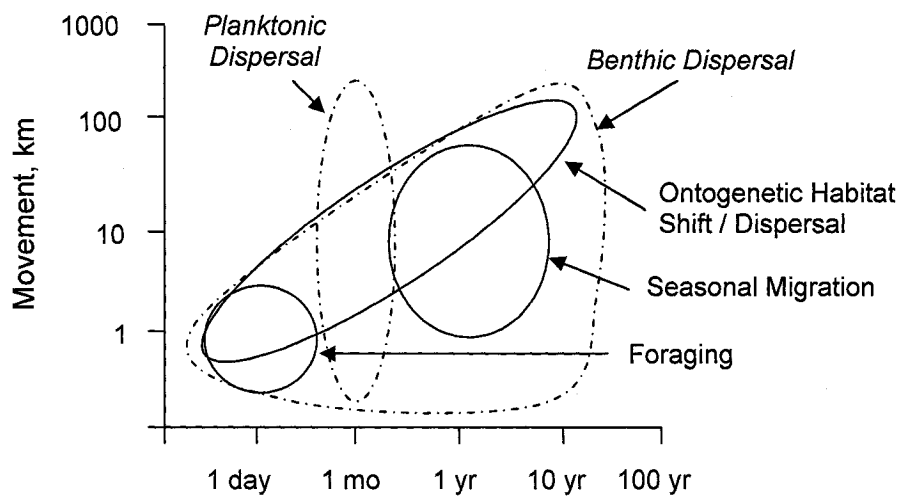
A. Space-Time Scale of Lobster Movement
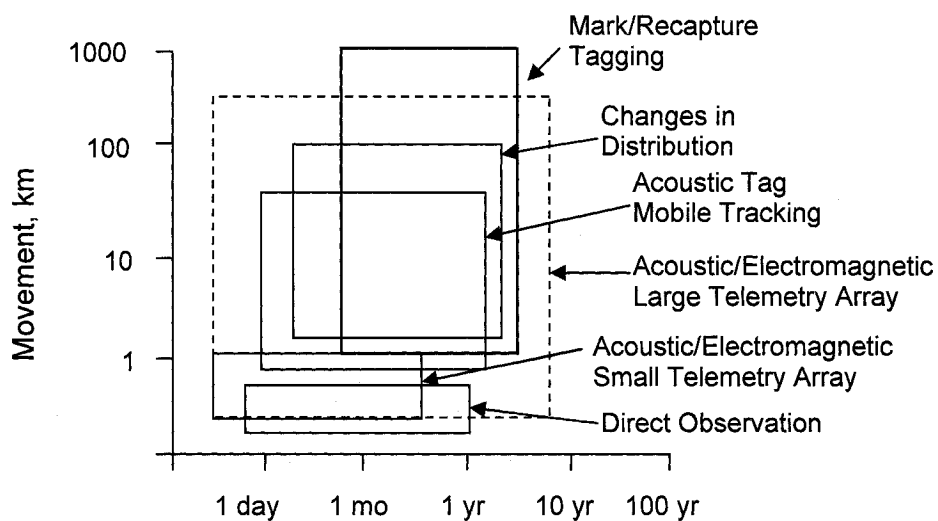
B. Space-Time Scale of Research Methods

Fig. 1.1. Temporal and spatial scale of lobster (*Homarus americanus*) movement patterns represented as envelopes on a graph of time vs. distance.

Winter ⬤

Summer ⬤

A. Seasonal Migration

Winter ◯◯

Summer ⬤

B. Partial Seasonal Migration

Winter ⬤

Summer ⬭

C. Dispersal into Seasonally
Available Habitat

Winter ◯◯

Summer ⬭

D. Partial Dispersal into
Seasonally Available Habitat
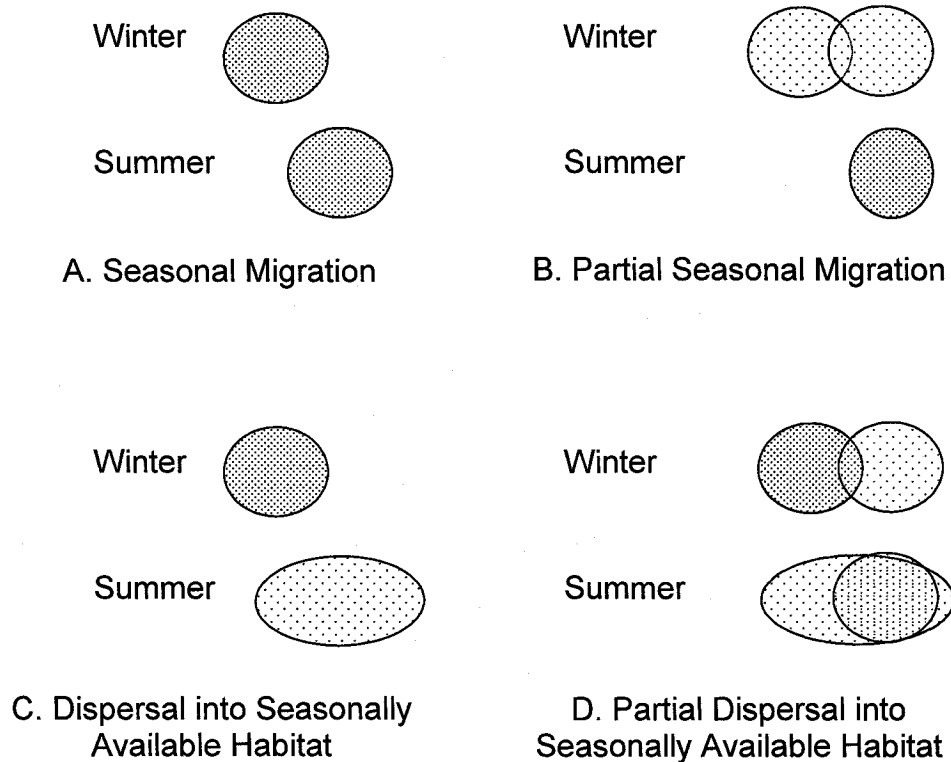
Fig. 1.2. Schematic of seasonal population redistribution from mass migration and dispersal of all or part of the population. Population density if represented by the density of dots. Seasonal population redistribution can result from migration of all the population between winter and summer habitat (A) or migration of part of the population (B), in this case only part of the population moves to different habitat for the winter. Seasonal population redistribution may also result from dispersal of a population into seasonally available habitat of all (C) or part (D) of the population.
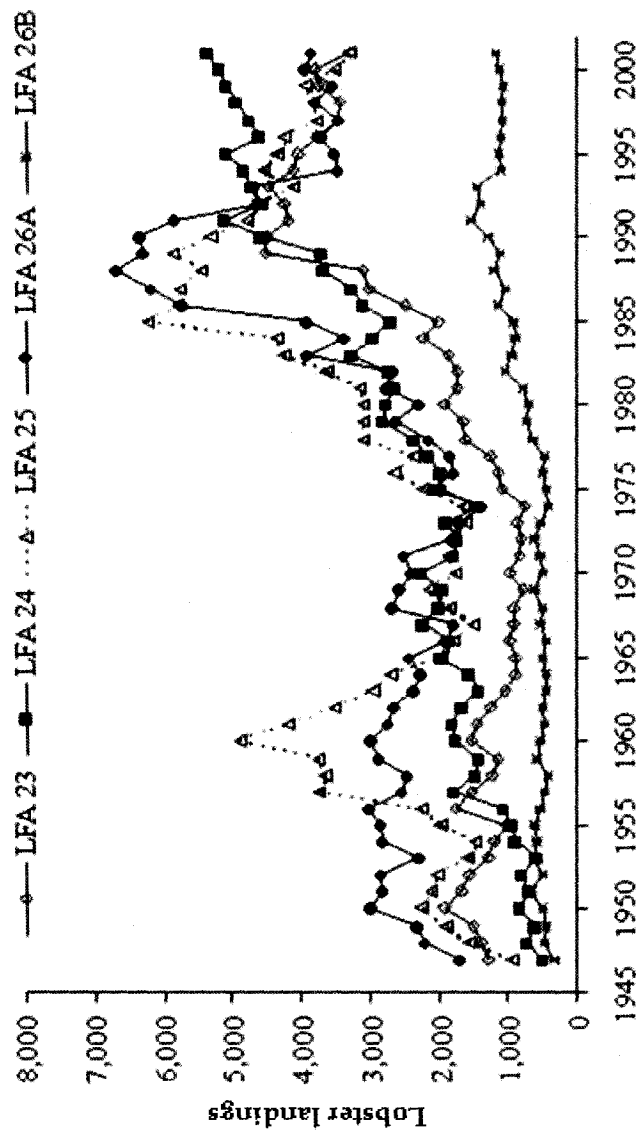
Fig. 1.3. Lobster landings (t) in the six lobster fishing areas (LFAs) of the southern Gulf of St. Lawrence. LFA 25 and LFA 26A are in the Northumberland Strait, between Prince Edward Island and Nova Scotia and New Brunswick; LFA 23, is on the north side of Prince Edward Island; LFA 24 is off of northern New Brunswick; LFA 26B is off the west coast of Cape Breton Island, Nova Scotia. Graphic modified from Canadian Stock Assessment Document 2002/05.

Canner:Market 3:1

Market

Canner

Sub-legal

Canner:Market 3:2

Market

Canner

Sub-legal

Reduced mortality   Immigration

☐ Survivor   ▦ Dead/emigrant   ▨ Immigrants

⇧ Survival   ➚ Emigration +
                  Mortality
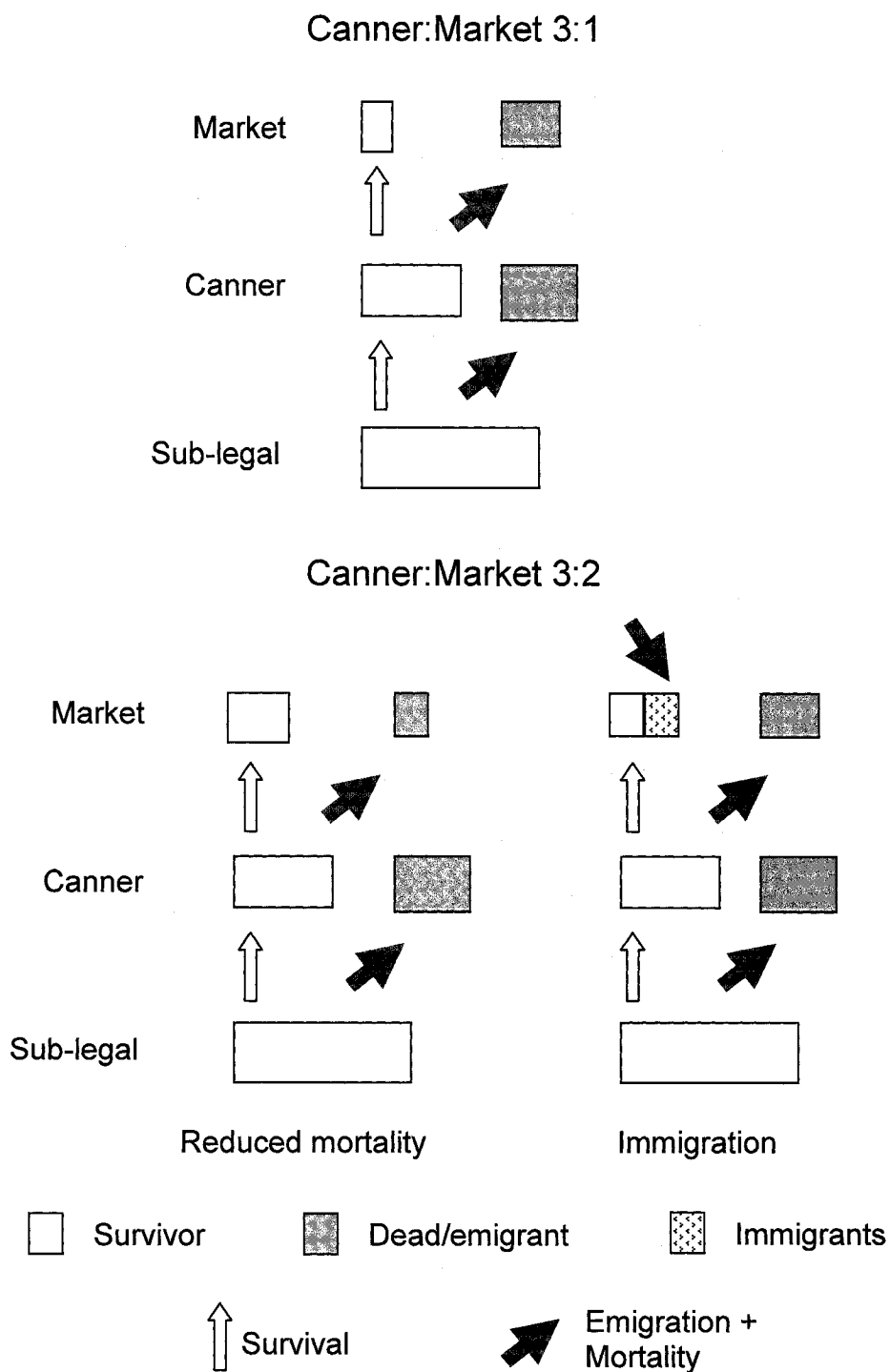
Fig. 1.4. Schematic of the influence of mortality and emigration on the ratio of abundance of different size classes. Low mortality and emigration rates result in a high proportion of large market-size lobster, here represented as 3:2 Canner:Market. Alternatively, immigration of large market-size lobster could increase the proportion of market-size lobster.

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CHAPTER 2

The Contribution of Migration to a Seasonal American Lobster (*Homarus americanus*) Fishery in Canada: an Experimental Trap Survey

Abstract

Seasonal changes in movement behaviour and spatial and temporal distributions of commercially exploited species affect both their availability and catchability. The distribution and size composition of commercial catches of American lobster (*Homarus americanus*) in Northumberland Strait, Gulf of St. Lawrence, Canada, suggest a seasonal immigration into the strait. A catch-and-release experimental trap survey conducted in June and July 2002 showed a 40-fold increase in lobster catches in the month preceding the local fishery, underscoring the importance of the timing of the fishing season to the success of the fishery. Catches increased initially in the north-west and sequentially toward the central part of the strait, supporting observations by fishermen and suggesting immigration from the north-west to the south-east. Water temperatures and, hence, the catchability of lobster increased during the survey. However, water temperature does not explain the pattern of increase as water warmed first in the south-east and subsequently in the north-west. The catch of both market-size ($\geq$ 81 mm CL) and smaller, canner- and sub-legal-size (< 81 mm CL) lobster increased during the survey. A change-in-ratio analysis estimated a 72% increase in the abundance of canner- and sub-legal-size lobster during the survey; a comparison of catches by trawl surveys before and after experimental fishing also indicates a 3-fold increase in lobster abundance. The migration implied by the change in abundance and distribution has not been identified by mark/recapture tagging studies in the strait. The mass movement of lobster into the central strait is consistent with an ontogenetic habitat shift away from larval settlement areas, density-dependent dispersal or directed inshore/offshore migration.

Introduction

Fisheries scientists develop models to predict population growth from survival and fecundity schedules. While immigration and emigration are recognized as important demographic processes, stock analysis is often simplified by working at scales large enough that the net flow of animals is assumed to be negligible (Ihssen et al. 1981). The development of the metapopulation approach to population dynamics has highlighted the importance of small-scale, within-population movement (Hanski 1999). Analyses of both Atlantic cod (*Gadus morhua*) (Hutchings 1996, Smedbol and Stephenson 2001, Beacham et al. 2002) and salmonid (Cooper and Mangel 1999) fisheries have revealed spatial variability in trends in the landings indicative of population structure that was not accounted for by management and conservation strategies, and that may have contributed to the collapse of these fisheries.

Since the 1980s, landings of American lobster (*Homarus americanus*) across its entire range (North Carolina to Newfoundland) have been increasing, but at smaller spatial and temporal scales, there has been variability in the landings (Miller 1994, Chadwick 1998). For example, the Northumberland Strait (Fig. 2.1), a shallow body of water separating Prince Edward Island from Nova Scotia and New Brunswick in eastern Canada, was the first area in the southern Gulf of St. Lawrence (sGSL) to experience increased landings. Since the mid-1990s, however, the landings have declined in the Northumberland Strait, while catches in the rest of the sGSL have been constant or have increased (Comeau et al. 2004). This decline in landings is of local social and economic importance and may also be indicative of future trends in the sGSL.

The population structure of American lobster is not known and efforts to use genetic markers have had limited success because of the long history of live transport of lobster for commercial and scientific activities (Harding et al. 1997). For more than 40 years, fishermen have argued that lobster migrate into the Northumberland Strait in the summer (Wilder 1963). Indeed, the only late-summer or fall fishing season in the sGSL was, in part, established to accommodate the belief that the lobster fishery inside the strait depended on the seasonal movement of lobster. The evidence supporting this position includes observations by divers, by-catch in other fisheries, changes in catch rates and a greater proportion of large market-size lobster (≥ 81 mm Carapace Length) in fisheries catches inside the strait, compared to outside of the strait. Contrary to this evidence for migration, tagging studies in the Northumberland Strait have consistently failed to demonstrate directed seasonal movement, and the observed increases in catch rates and variability in the size composition of the commercial catch have been attributed to increased feeding rate of post-moult lobster, warmer water temperatures, and local differences in fishing practices (Templeman 1936, Wilder 1963, Comeau and Savoie 2002).

Seasonal changes in the distribution and abundance of lobster in the nearshore has been documented by commercial landings, and experimental trap and trawl surveys. Seasonal inshore-offshore movement may be part of a seasonal directed migration into warm water for moulting and mating (Bergeron 1967, Munro and Therriault 1983, Moriyasu et al. 1998) or undirected dispersal into seasonally available habitat (Jeffries and Johnson 1974, Howell et al. 1999, Watson et al. 1999) or sub-optimal habitat

(Karnofsky et al. 1989b). While directed offshore movements may avoid low salinity in estuaries (Jury et al. 1994a, 1994b, Howell et al. 1999, Watson et al. 1999), increased wave action (Ennis 1984, Jeffries and Johnson 1974), or ice scour (Thomas and White 1968).

Individual lobster tracks have also demonstrated seasonal inshore-offshore movement. Lobster with acoustic tags, positioned every three days in a New Hampshire estuary, alternated between station keeping or homing behaviour and directionally persistent movement, which combined resulted in a wandering into the estuary (Watson et al. 1999). Multiple recaptures of tagged ovigerous females show seasonal onshore-offshore migration off of Nova Scotia (Campbell 1986, Pezzack and Dugan 1986), which appears to be associated with the maintenance of optimal temperatures for egg development (Campbell 1986).

In the present study, both trap and trawl surveys were used to identify migration through a change in lobster abundance in the central part of Northumberland Strait prior to the fishing season, which extends from August through October. The work was completed with the support of local fishermen and the fishermen's organizations. Cooperation with fishermen has proven to be valuable in fisheries research and contributes to better participation in management decisions and practice (Neis et al. 1999, Hutchings and Ferguson 2000). Additionally, experimental fishing by commercial fishermen contributes to a shared understanding of the lobster resource and benefits from existing expertise, boats and gear.

Methods

Study Area

The Northumberland Strait separates Prince Edward Island from New Brunswick and Nova Scotia on the southern edge of the Gulf of St. Lawrence (GSL). It is approximately 320 km long and between 13 and 48 km wide. The sediments are composed of glacial tills, relict gravels, sands and silts. Water flows from west to east. Tides inside the strait are mixed or diurnal with a maximum 2 m tidal range (Davis and Browne 1996). During summer, bottom water temperatures can approach 20 °C inside the strait. Warming of the water inside the strait is accelerated by sand flats exposed during low tides. As a consequence, bottom water temperatures increase initially in the central part of the strait and then to the east and west (Petrie et al. 1996). In winter, ice covers much of the strait, and ice scour can affect the benthic community (Davis and Browne 1996). Keel depths of ice ridges vary annually and spatially, with keel depths as deep as 16 m, but more typically of about 1 to 2 m (Brown et al. 2001).

In the present study, the central strait was defined as the area between the Confederation Bridge and a line between Saint-Eduoard-de-Kent, New Brunswick, and West Point, Prince Edward Island (Fig. 2.1).

Trawl Survey

The Department of Fisheries and Oceans, Canada, (DFO) conducted trawl surveys before and after the lobster fishery in the Northumberland Strait in 2001 and 2002. Trawl stations were established on a 3.1 km (2 nautical miles) grid for all bottom suitable for

the trawl deeper than 4 m. A No. 286 trawl with rockhopper footgear was towed for 15 minutes at 4.6 km (25 nautical miles) per hour at stations chosen randomly in five strata defined by bottom type. The net had a 17.7 m (58 ft) head rope and a 21.9 m (72 ft) ground rope. The trawl gear is described in more details by Comeau et al. (2004).

Experimental Trap Survey

Experimental traps were fished at four locations inside the central part of Northumberland Strait (Fig. 2.1). At each location, one station of shallow hard bottom between 7.4 and 9.1 m deep (Station 1: 20-30 ft) was chosen by the fishermen and three other stations were chosen at random in each of three other depth strata positioned along a transect extending from the shallowest to the deepest stations. The depth categories of Stations 2 through 4 were 9.1-12.2 m (30-40 ft), 12.2-15.2 m (40-50 ft), and 15.2-18.3 m (50-60 ft), respectively. There were 4 transects, with 4 stations, and 8 traps per station. In total, 128 traps were fished. Traps were set during the second and third week of June 2002, and hauled 3 times a week for 4 to 6 weeks (Table 2.1).

Data collected from the traps included characteristics of the lobster and the by-catch. Lobster carapace length (CL) was measured from the eye socket to the end of the cephalothorax in a line parallel to the mid-dorsal line. Sex, the presence or absence of eggs and egg stage, and missing or regenerating chelae were also recorded. Before release, each lobster was marked either with a band on a claw knuckle or a streamer tag sewn into the dorsal musculature between the carapace and tail. Multiple bands and streamer tags made it possible to identify lobster that were recaptured during the trap

survey. The number of rock crab (*Cancer irroratus*) and lady crab (*Ovalipes ocellatus*), and the presence of fish and other invertebrates in traps were recorded.

Trap design differed between transects (Table 2.2) but was constant within transects. The escape vents were blocked on all traps to increase the probability of catching smaller lobster. The bait used was either salt herring (*Clupea harengus*) and/or gaspereau (*Alosa pseudoharengus*) and was supplemented by rock crab caught in the traps. Cable ties were often used to confirm that traps had not been fished between hauls. To minimize the effect of soak time, traps were hauled every 2 to 4 days. VEMCO® (Shad Bay, Nova Scotia, Canada) data loggers recorded temperature every two hours at all but three stations (Table 2.1).

The Maritime Fishermen's Union and the Prince Edward Island Fishermen's Association identified local fishermen for the trap survey. Two of the four fishermen had previous experience with lobster research. Fishermen agreed to use their own boats and gear and to follow the experimental protocol. A stipend was offered to cover the cost of bait and fuel. Gear conflict with the herring fishery and the loss of traps resulted in some minor modifications to the protocol. At Robichaud, Station 3 and Station 4 were not fished on June 21, and between July 1 and July 8 Station 3 was not fished. In Egmont Bay, only 30 traps were hauled between July 1 and July 5, as the two deepest traps (Station 4) were lost. In Bouctouche, the carapace lengths were not measured on July 8 and 10 and on those days 22 lobster were released without bands.

Statistical Analyses

Statistical analyses were completed using S-plus Professional Edition 6.1.2. Paired and unpaired t-tests were used to compare mean trawl catch before and after the trap survey, and the catch of lobster and crab in traps in Egmont Bay, where trap construction affected the rock crab, but not the lobster, catch. Community composition between the locations and the depths was compared using Sorensen's coefficient of similarity (S; Krebs 1999). A Chi-square contingency test was used to compare the ratio of male to female lobster in the first (June 24) and last weeks of the survey (July 24). Correlations between the mean lobster catch per trap per station, mean crab catch per station, temperature, day of year, and soak time were calculated with linear models; the linear model of the median daily temperature included day, location and depth.

A generalized linear model of the lobster catch per station (Poisson distribution) with day, location, depth and the interactions between day and location and day and depth as fixed effects and station as a random effect was used as the maximal model. The intercept was allowed to vary randomly with station to account for the repeated measures. The stratified and arbitrary selection of locations along the strait could have biased sampling, but I can think of no reason why this would be the case. However, the shallow stations were chosen by the fishermen, which could have contributed to a depth effect, as the fishermen may have identified areas with higher catch rates than the randomly-chosen deeper stations. The model including the interaction between location and depth could not be fit. And, because there were missing temperature data and temperature did not improve the maximal model, temperature was not included. A log- likelihood ratio test

was used for model simplification and identification of significant differences between locations by grouping the factors (Crawley 2002).

Maximal model: Lobster ~ day + location + depth + day:location + day:depth, offset logarithm (number of traps) + logarithm (soak time)

Change-In-Ratio Analysis of Immigration and Recruitment

Minimum levels of immigration and recruitment of lobster were estimated from a change-in-ratio analysis of the composition of trap data (Claytor and Allard 2003). This method is commonly used to estimate exploitation rate. We use it here to estimate immigration and recruitment. In this analysis, the abundance of the larger market-size ($\geq$ 81 mm CL) lobster was assumed to be constant (reference class) and immigration and recruitment of canner- and sub-legal-size canner- and sub-legal-size ($<$ 81 mm CL) lobster (focal class) was estimated under the assumption that the ratio of catchability of market-size and canner- and sub-legal-size lobster does not change.

The proportion of the catch comprised of canner- and sub-legal-size lobster during in a given sampling period (j) was:

$$p_j = c_{cj} / (c_{cj} + c_{mj})$$

where the catch of canner- and sub-legal-size lobster during period j is c_{cj}, and the catch of market-size lobster is c_{mj}. A simple end-point comparison for immigration and recruitment rate (IR) compared the ratio of the catch in the week of June 24 (p_o) and July 24 (p_j) for all sites and stations (Table 2.4):

$$IR_{\text{end points}} = 1 - (p_j/1-p_j) / (p_o/1-p_o)$$

Results

Trawl Survey

The trawl survey caught three times as many lobster in July/August 2002 than in either May 2002 or October 2001 (Table 2.3). As the area swept by a tow is a function of water depth (Somerton et al. 2002), a paired t-test incorporating those stations sampled both in the May and the July/August surveys provided a more robust, although more geographically limited, comparison of lobster abundance (Fig. 2.1). The paired t-test (mean difference=14.84, t=4.2969, df=25, p<0.001) also indicated a 3-fold increase in lobster catch.

Experimental Trap Survey

The catch of lobster per trap ranged from zero to 26. Very few lobster were caught more than once during the survey (Table 2.1), indicating a large or mobile lobster population at all locations. The catch of both canner- and sub-legal-size and market-size lobster increased during the survey (Fig. 2.2). In the week of June 24, an average of 0.12 lobster were caught per trap and an average 5.23 were caught per trap in the week of July 24. The change-in-ratio calculations indicate that 72% of the catch in the week of July 24 was comprised of immigrants or new recruits (Table 2.4). The ratio of male to female lobster was greater during the last week of the survey (559:445, 1.3) than in the first (23:28, 0.8), although the difference was not significant (Chi-square=1.79, p=0.181).

The catchability of lobster can be affected by interspecific interactions (Miller 1990). Catch rates of rock crab (*Cancer irroratus*), the most abundant by-catch species,

ranged from zero to 384 per trap. Crab catch declined during the survey (Fig. 2.3) and

was significantly negatively correlated with lobster catch per trap. In Egmont Bay, crab

catch was also negatively correlated (p<0.001, df=54) with lobster catch, but a

comparison of the catch of lobster and crab in the traps with different designs (Table 2.1)

suggests that the lobster were not affected by the presence of crab. There was no

difference in the lobster catch between the wire and wooden traps paired by depth and

day (mean difference=0.11, t=0.601, df=55, p=0.550), even though the wire traps

captured significantly fewer rock crab (mean difference=-52.45, t=-9.396, df=55,

p<0.001). The by-catch of the traps included starfish (echinoderms), winter flounder

(*Pseudopleuronectes americanus*), cunner (*Tautogolabrus adspersus*), sculpins (Cottidae

sp.) and other fish, including tomcod (*Microgadus tomcod*) and Greenland cod (*Gadus

ogac*). There was very little difference in the by-catch at all stations (0.9333 ≥ S ≤ 1.000)

and locations (0.7692 ≥ S ≤ 1.000).

Lobster catch per station was positively correlated with bottom water temperature

(Fig. 2.3). Between the middle of June and late July, bottom water temperature increased

from between 10 and 14 °C to between 18 and 19 °C (Fig. 2.4). In the north-west

(Bouctouche, Egmont Bay and Robichaud), there was a reduction in bottom water

temperature that followed a period of high winds that may have caused an intrusion of

colder deep water. Although there is some variability in the increase of water

temperature, the water was generally warmer in the most eastern site, Murray Corner,

than in the sites to the north-west (Table 2.4, Fig. 2.5).

Traps were hauled every two to three days, except on two occasions when the

soak time was four days. There was no significant correlation between soak time and

catch (Fig. 2.3). Nonetheless, near the end of the survey, when catches were high, trap saturation may have occurred. Trap saturation would limit the peak catch and hence provide a conservative estimate of any changes in abundance, recruitment and catchability.

Plots of the catch per trap per station showed increasing catch rates at all locations, such that the catch exceeded 2 lobster per trap first in the westernmost site and then sequentially to the east (Fig. 2.5).

Mixed-Effects Model

The maximal model of the lobster catch per station (Poisson distribution) included 3 fixed variables: day of year (standardized to the first day of the survey, day of year – 172), location (1 to 4 factor), and depth (1 to 4 factor); interactions between day and location and day and depth were also included in the model. Depth did not significantly improve the fit of the model but day of year, location and the interaction between day of year and location did (Table 2.6).

Minimal model: Lobster ~ day + location + day:location, offset logarithm (number of traps) +logarithm (soak time)

A post-hoc test of the location effect, using log-likelihood ratio tests (Crawley 2002), did not detect a difference in lobster catch per station between the two sites to the west, Bouctouche and Egmont Bay, and the two sites to the east, Robichaud and Murray Corner (Table 2.7).

Discussion

Changes in lobster movement behaviour and distribution, as inferred from experimental trap and DFO trawl surveys, reveal seasonal migration into Northumberland Strait. Both abundance and catchability of lobster increased in the central part of the strait in the month of July. The remarkable increase in lobster catch in the weeks preceding the fishery demonstrates the importance of the timing of this fishery. A comparison of the trawl catches in May and July and a change-in-ratio analysis of the experimental trap catches suggested that lobster abundance increased three-fold. The sequential increase in catch during the trap survey from north-west to the south-east is strongly suggestive of a seasonal, migration of lobster into the central part of the strait from the north-west. These data are consistent with sequentially increasing commercial landings along the strait observed by fishermen and other evidence for migration of lobster into the Northumberland Strait. While this evidence of lobster movement within LFA 25 does not draw into question the definition of the lobster management units, it does underscore the importance of movement to the management of the fishery through the definition of the fishing season.

The experimental trap survey design was able to detect changes in distribution and abundance over months and several 100's of kilometres. Experimental traps can sample a larger area than dive surveys and are more flexible than trawl surveys that cannot be used on rocky bottom and are prohibitively expensive for use over extended periods of time. Trap catches are also familiar to both fishermen and scientists and more readily compared to and interpreted with respect to commercial landings. However,

variability in lobster behaviour and, hence, catchability may contribute to the increased catch rates.

The change-in-ratio analysis indicated a 20-fold increase in catchability. It has been argued, that high catch rates in the central part of the strait result from an increase in the catchability of lobster in the fall, when water temperatures are high (Templeman 1936, Wilder 1963, Comeau and Savoie 2002). Acclimatized lobster from the New England coast in tanks with stable thermal gradients preferred water between 13 °C and 19 °C with a peak at 16.5 °C (Crossin et al. 1998). The bottom water temperatures in the central part of the strait increased from 12 °C to 14 °C to almost 18 °C between late June and July, 2002 (Fig. 2.4). However, the water temperatures increased first in the south-east and then in the north-west, a direction opposite to that observed for the increases in lobster catch. Nonetheless, temperature is positively correlated with catch and probably contributes to high catchability of lobster by the end of the survey, but does not explain the sequential increase from northwest to southeast.

Post-moult feeding might also contribute to the increased catchability of lobster in July (Templeman 1936, Miller 1990, Tremblay and Eagles 1997, Tremblay and Smith 2001). During ecdysis and the stages immediately following the moult lobster feeding may be reduced (Aiken and Waddy 1980), although unpublished gut contents suggest that soft lobster in the Northumberland Strait are feeding (JM Hanson, personal communication). In the present study, the catch of lobster was low for the first 2 to 4 weeks (Fig. 2.4). If the non-feeding moult stages (A_1, A_2, and B) comprise 3.4% of the intermoult period (Aiken and Waddy 1980), then reduced catches would be expected to last only 4 to 5 days. There was also no difference in the incidence of soft lobster among

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locations or depths (Table 2.6). Again, while post-moult feeding may contribute to increased catchability, it cannot account for the pattern of increased catch from north-west to south-east.

Templeman (1936) noted that the increase in catch in his experimental traps consisted of mostly newly shelled lobster, and suggested that low catch rates in early July occurred during the moult. He interpreted the initial reduction in the catch per trap per day of soak time as reduced feeding during the moult. However, the high initial catches result from standardization of catch per trap to soak time; catch per trap per day of soak is asymptotically related to soak time (Miller 1990). The short, one- and two-day soak times at the beginning of the 1932 survey produced a higher catch per trap per day than the longer soak times later in the survey. I have plotted Templeman's data as catch per trap (Fig. 2.6). Despite variability in soak time, bait and trap design, these data correspond to the catch per trap observed in an experimental trap survey in Egmont Bay in 1981 (Jamieson and Campbell 1985), this study, and my preliminary research in 2001. Together these data suggest that an increase in lobster abundance, recruitment and catchability in July is characteristic of the central strait.

The similarity in by-catch species composition between the trap survey locations suggests that neither habitat nor trap design affected the catch composition. The most abundant by-catch species was rock crab. Richards et al. (1983) showed that there was no difference in lobster catch between empty traps and those containing 3 and 8 rock crabs, whereas lobster-loaded traps inhibited crab catch. Although the blocked escape vents in the present study resulted in rock crab catches that greatly exceeded those used in the Richards et al.'s (1983) study, a comparison of lobster and crab catches in Egmont

Bay confirms this result. Lobster catch was unrelated to the presence of crab, but the crab catch was reduced in the presence of lobster. In this area, rock crab are more than 50% of the diet of lobster (J.M. Hanson personal communication), hence, rock crab may avoid or leave traps that contain lobster.

Seasonal inshore-offshore movements of lobster are common in shallow bays and estuaries in Quebec (Bergeron 1967, Munro and Therriault 1983), Prince Edward Island (Jeffries and Johnson 1974, Moriyasu et al. 1998) and New England (Howell et al. 1999, Watson et al. 1999). The strongest evidence for the inshore-offshore migration lobster is inferred from changes in the distribution, documented by commercial landings, experimental trap, SCUBA, and trawl surveys. A larger proportion of large lobster in landings in the Northumberland Strait than outside the strait (Lanteigne et al. 1998 and 2002) suggests immigration. Similarly, differences in the distribution of mature male and female lobster indicate of sex-biased movement (Bergeron 1967, Munro and Therriault 1983, Howell et al. 1999). Direct evidence for migration based on individual lobster movement is less common. Multiple recaptures of tagged ovigerous females have revealed seasonal inshore-offshore migration off of Nova Scotia (Campbell 1986), but multiple recaptures of this commercially valuable and intensely fished species are not abundantly available in inshore waters. However, one study of lobster tracked with acoustic tags in New Hampshire, found a tendency for movement out of the estuary in the fall and into the estuary in the spring (Watson et al. 1999).

The change in lobster distribution and abundance documented by the experimental trap and trawl surveys suggest a pattern of movement that had not been identified by studies of tagging experiments in the Northumberland Strait, which find no

directional bias in the displacement of lobster between release and recapture (review

Comeau and Savoie 2002). Ice scour, fall storms and the lack of cover may make the

Northumberland Strait unsuitable for overwintering lobster. Migration into the strait in

July may be part of a directed to and fro seasonal migration or undirected dispersal or

diffusion. Dispersal could be density or shelter dependent (Steneck 2006) and/or part of

an ontogenetic habitat shift, such as that which has been documented in blue crab

(*Callinectes sapidus*) (Pardieck et al. 1999) and spiny lobster (*Panulirus argus*) (Lipcius

et al. 1997). On the Atlantic coast, where surveys of settlement and juvenile lobster have

been undertaken, settlement hotspots have been identified (Steneck and Wilson 2001).

This produces a high degree of spatial variability in the abundance of juveniles on the

large scale (Palma et al. 1999). High-density settlement areas or hotspots may set the

stage for density-dependent dispersal of juvenile and adult lobster.

Further research on larval and adult dispersal and on the distribution of early

benthic phases will be necessary to assess population structure and whether the decline in

lobster landings in LFA 25 results from processes unique to this area. Dispersal could

produce source-sink population dynamics (Pulliam 1988, Pulliam and Danielson 1991,

Hudon et al. 1991, Morris 1991), or the observed mass movement may also be part of an

ontogenetic shift of a single population from settlement areas to an adult distribution.

Unfortunately most data on lobster distribution and abundance are fishery-dependent and

limited to specific size classes and, in Canada, to particular seasons. Data on the

distribution of smaller size classes and during seasons other than those encompassed by

the fishery could help to determine whether the mass movement documented here is part

of a directed inshore/offshore movement, a spatially arbitrary ontogenetic habitat shift, or

density-dependent dispersal. A comprehensive approach, which combines the study of individual movement and population abundance and distribution, is necessary to fully understand population structure and its consequences for population dynamics.

Table 2.1. Summary of experimental trap catch and effort at four locations in the central part of the Northumberland Strait in 2002.

	Bouctouche	Egmont Bay	Robichaud	Murray Corner
Number of days traps hauled	8	14	15	16
Survey period	Jul 1 – Jul 17	Jun 26 – Jul 26	Jun 23 – Jul 26	Jun 21 – Jul 26
Total trap hauls [1]	318	470	528	544
Total lobster (*Homarus americanus*)	476	1151	603	453
Range of lobster carapace length, mm	55-121	52-147	51-135	56-137
Lobster caught twice	3	16	2	17
Lobster caught three times	3	2	0	0
Per cent of lobster caught more than once [2]	1.2–5.9	1.6	0.3	3.7
Total crab (*Cancer irroratus*)	20691	26482	27693	32769
Stations for which temperature data are available	1, 2, 3, 4	2, 3, 4	1, 4	1, 2, 3, 4

[1] Robichaud: Traps at Stations 3 and 4 were not fished on June 21, and traps at Station 3 were not fished on July 1, July 3, July 6 and July 8 because of gear conflict.

Egmont Bay: Traps 31 and 32 (Station 4) were lost. There are no data from these traps on year July 5, July 8, July 10, July 12 and July15.

[2] Bouctouche: Carapace length of the 88 lobster caught on July 8 and July 10 were not measured and 22 lobster were released without bands or tags. The range in lobster recaptured is calculated with the recapture of between zero and 22 of those released without bands.

Table 2.2. Summary of trap design and fishing methods.

	Bouctouche	Egmont Bay	Robichaud	Murray Corner
Number of parlours	2	1	2	2
Mesh (inches)	1.5 wire	1.5 wire / twine [1]	1.5 wire	1.5 wire
Length (inches)	48	48	48	48
Width (inches)	21 or 24	32	21	24
Depth (inches)	12 or 13.5	20	16.5	21
Parlour length (inches)	16.5	20	16.5	21
Bait	herring	gaspereau	gaspereau	herring
Traps per buoy	1	2	1	1

[1] At each station four wire and four wood and twine mesh traps were set.

Table 2.3. Comparison of the mean number of lobster per km towed during the October 2001, May 2002, and July and August 2002 trawl surveys.

	No. per km	n	t	df	p
October 2001	3.80	29	0.4584	64	0.6428
May 2002	4.41	37	-3.8163	88	0.0003
July/August 2002	12.07	53			

Table 2.4. Calculation of the immigration and recruitment rate (IR) from mean lobster caught per trap in the week of June 24 and the week of July 24.

	June 24 c_o	July 24 c_j
All	0.12	5.23
Canner and Undersized (< 81mm CL)	0.06	4.09
Market (≥ 81mm CL)	0.06	1.13
p	0.5	0.22
p / (1 − p)	1	0.28
IR	0.72	

Table 2.5. Summary of the linear model of median daily temperature (°C) by day of year, location and depth.

	Value	SE	df	p-value
LogLik		-437.4298		
SD Intercept		0.4889		
SD Residual		0.7478		
Intercept	13.2032	0.3905	359	<0.0001
Day – 172	0.1436	0.0043	359	<0.0001
Location2	0.9959	0.4070	6	0.0500
Location3	0.4501	0.4751	6	0.3801
Location4	1.7264	0.3668	6	0.0033
Depth2	-0.7077	0.4572	6	0.1726
Depth3	-1.5937	0.4572	6	0.0130
Depth4	-1.7268	0.4046	6	0.0053

Number of Observations: 373

Number of Groups: 13

Table 2.6. Model simplification of generalized linear mixed-effects models, fit by maximum likelihood to predict number of lobster caught per station. The catch was a Poisson distribution and the logarithm of the number of traps was an offset. Station was a random effect.

	Maximal Model				Location Model			
LogLik	-277.3532				-279.9659			
SD Intercept	0.25697				0.3303			
SD Residual	1.9751				1.9862			
	Value	SE	df	p-value	Value	SE	df	p-value
Intercept	0.1970	0.5446	185	0.7179	-0.2748	0.4829	188	0.5700
Day – 172	0.1388	0.0222	185	<0.0001	0.1450	0.0204	188	<0.0001
Location2	-0.9624	0.5968	9	0.1413	-0.9720	0.6079	12	0.1358
Location3	-1.0234	0.6629	9	0.1571	-1.1560	0.6710	12	0.1106
Location4	-0.4683	0.6305	9	0.4766	-0.6045	0.6367	12	0.3611
Depth2	-0.4122	0.5220	9	0.4500				
Depth3	-0.4545	0.5348	9	0.4373				
Depth4	-1.5068	0.5813	9	0.0291				
Day:Location2	0.0164	0.0233	185	0.4824	0.0183	0.0230	188	0.4287
Day:Location3	-0.0026	0.0252	185	0.9163	0.0032	0.0249	188	0.8961
Day:Location4	-0.0316	0.0247	185	0.2010	-0.0257	0.0242	188	0.2889
Day:Depth2	0.0019	0.0173	185	0.9108				
Day:Depth3	0.0038	0.0176	185	0.8301				
Day:Depth4	0.0407	0.0189	185	0.0330				

Number of Observations: 208

Number of Groups: 16

Table 2.7. Summary of post-hoc analysis of the mixed-effects model predicting number of lobster caught per station. Grouping locations together finds there to be no difference between the two most easterly sites and no difference between the two most westerly sites.

	Value	SE	df	p-value
LogLik	-283.1448			
SD Intercept	0.4026			
SD Residual	1.9961			
Intercept	-0.7957	0.2808	190	0.0051
Day – 172	0.1559	0.0089	190	<0.0001
Eastern Sites	-0.3521	0.4251	14	0.4214
Day-172:Eastern Sites	-0.2215	0.0130	190	0.0900

Number of Observations: 208

Number of Groups: 16
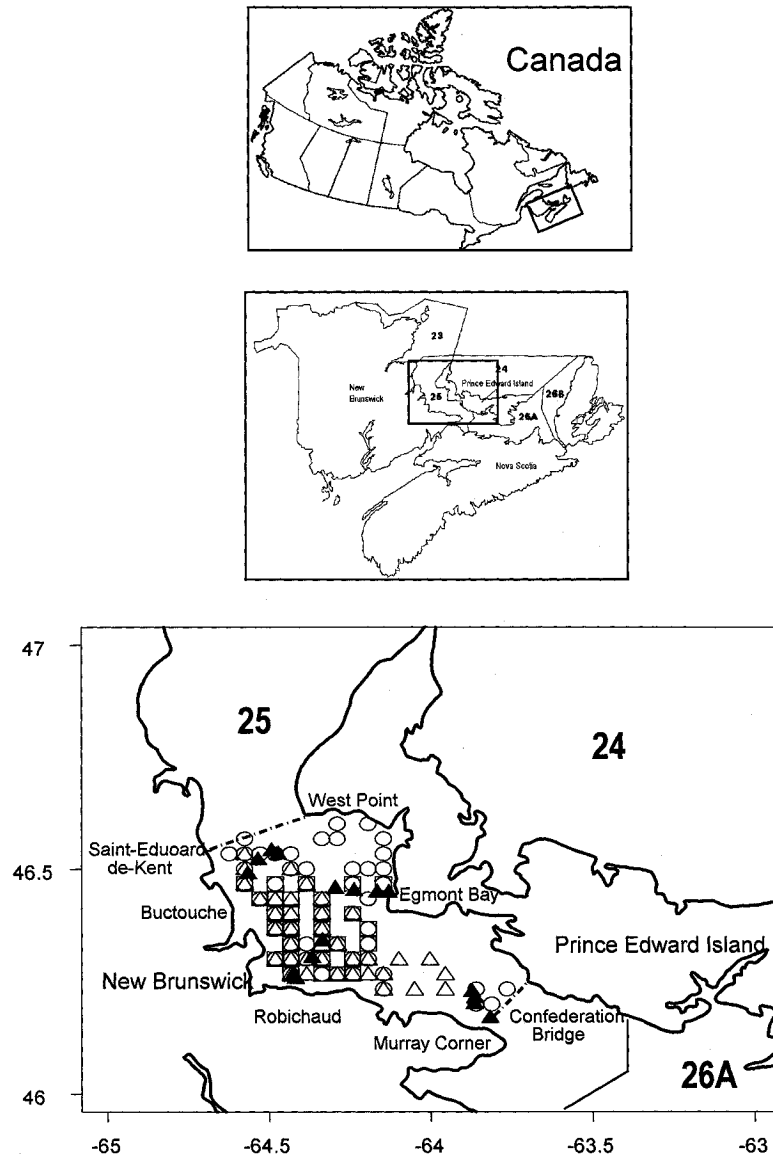
Fig. 2.1. Maps of Canada, the lobster fishing areas (LFAs) of the southern Gulf of St. Lawrence and the trawl and experimental trap survey locations in the central Northumberland Strait in October 2001 and the summer of 2002. Trawl Survey: △ 29 stations in Oct. 2001, ☐ 37 stations in May 2002, ○ 53 stations in July and August 2002. ▲Trap Survey 2002. Dashed lines delineate the boundaries of the central strait.
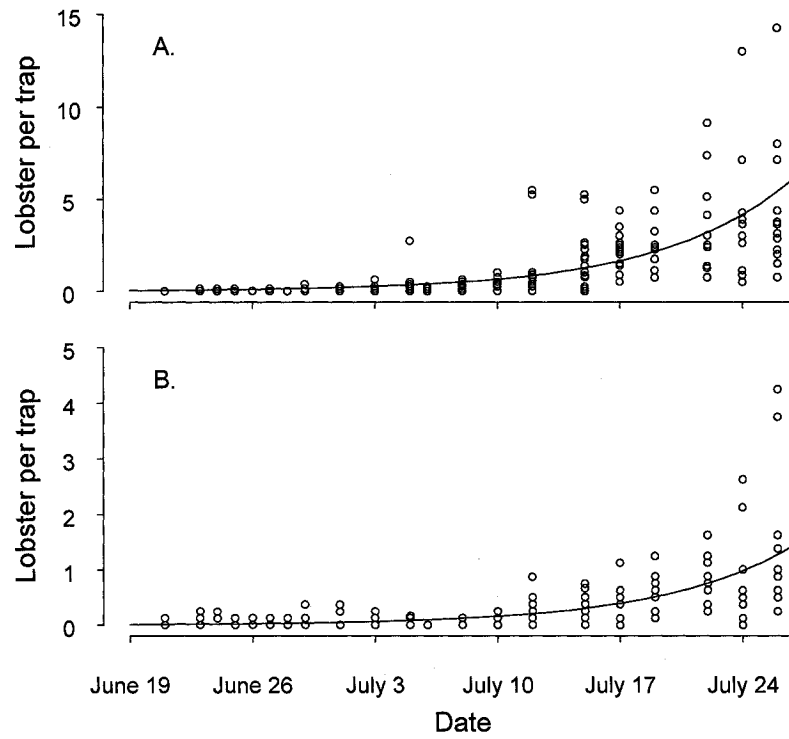
Fig. 2.2. Catch of canner- and sub-legal-size (< 81 mm CL) lobster (A) and market-size (≥ 81 mm CL) lobster (B) per trap plotted against date. The solid lines represent the general linear models: Catch ~ Date, family=Poisson, p<0.001, n=200.
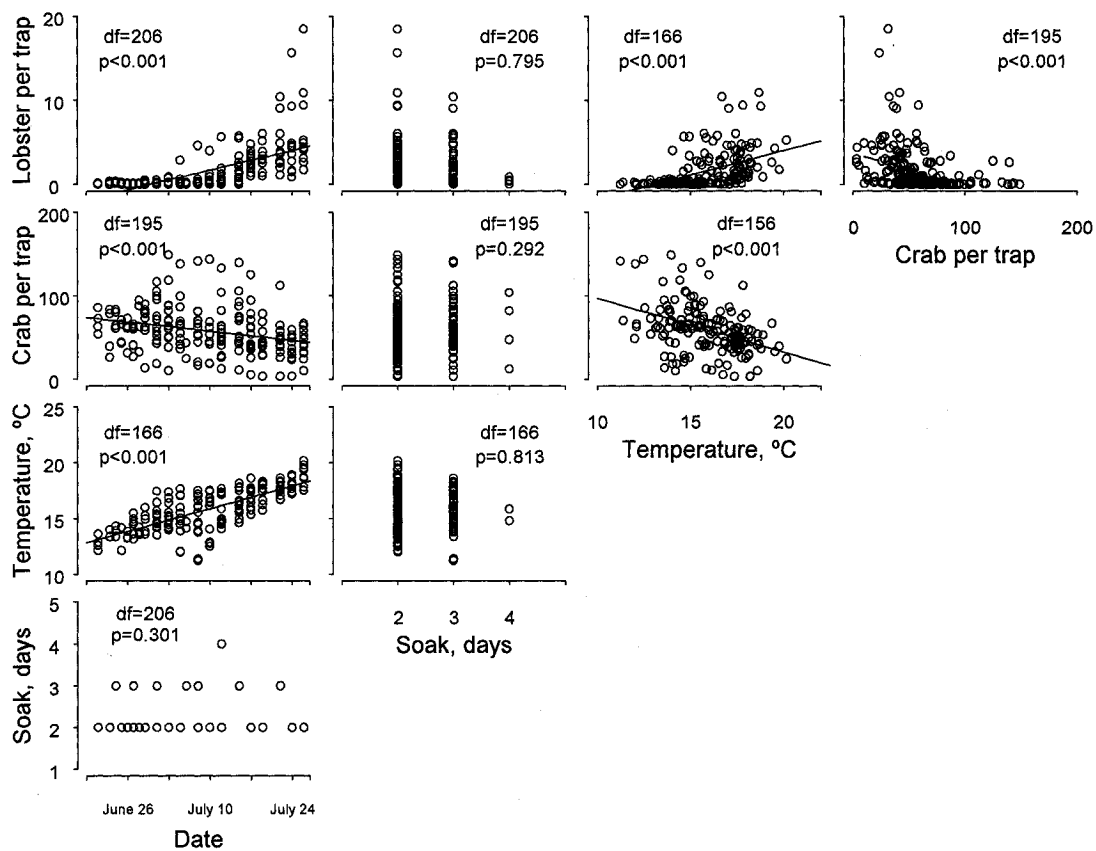
Fig. 2.3. Plots of mean lobster and crab catch per trap for each station at all four locations against day of year, temperature (°C) and soak time (d) at the four locations.
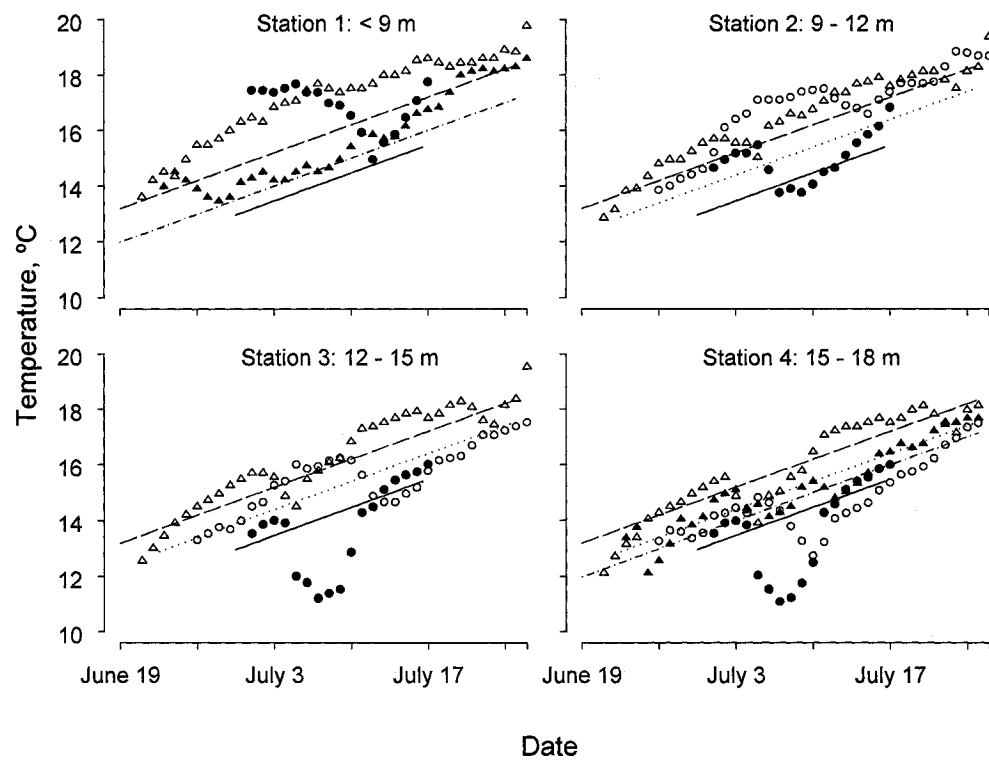
Fig. 2.4. Bottom water temperature (°C) at each station at each location plotted against date. There were four stations from which no data were obtained: ● Bouctouche, ○ Egmont Bay, ▲ Robichaud, and △ Murray Corner.
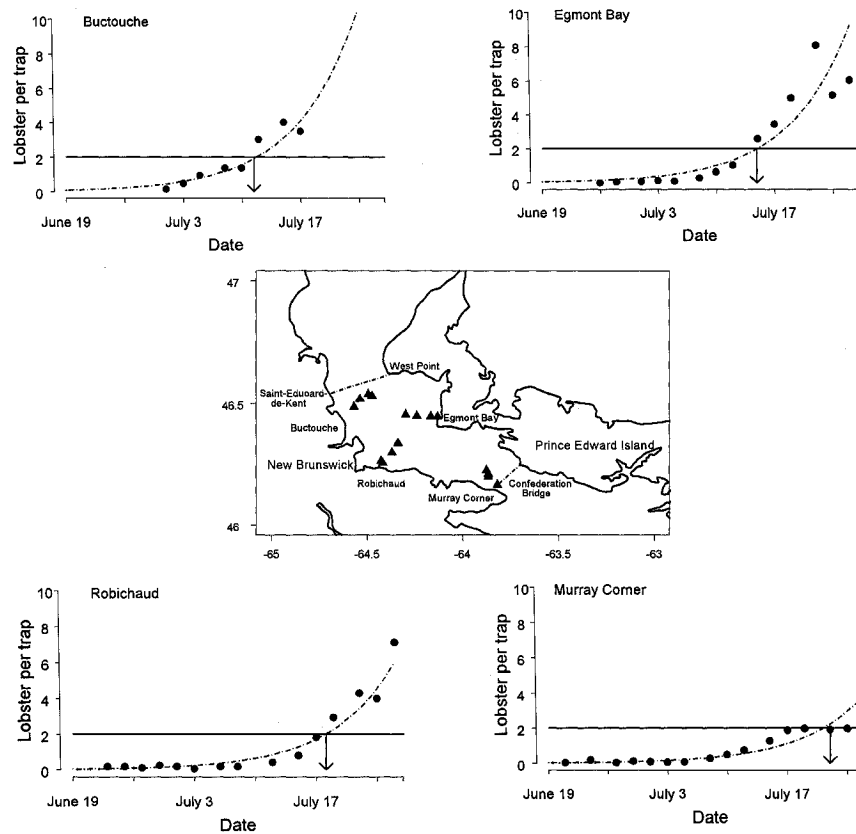
Fig. 2.5. Plots of mean lobster catch per trap at each location. The fitted lines are generated from a generalized linear model of mean catch by day of year. Neither temperature nor the station random effects are included in the model. The horizontal line is at 2 lobster/trap. The arrows indicate the date at which the catch exceeds 2 lobster/trap.
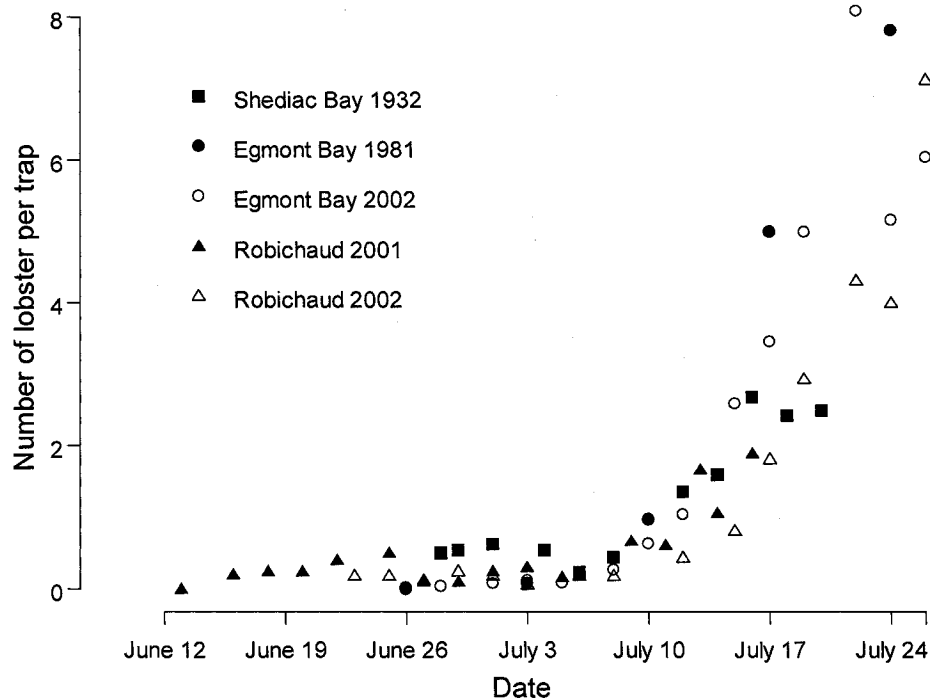
Fig. 2.6. Lobster catch (number per trap) in experimental traps in Shediac Bay in 1932 (Templeman 1936), Egmont Bay in 1981 (Jamieson and Campbell 1985), preliminary research in Robichaud in 2001, and Egmont Bay and Robichud in 2002. In Shediac Bay, between 24 and 47 traps were fished in June and July of 1932. In Egmont Bay there were between 200 and 402 trap hauls per week. In Robichaud in 2001, 18 or 20 traps were fished and in Egmont Bay and Robichaud in 2002, 32 traps were fished.

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CHAPTER 3

**Female-Biased Movement and a Correlated Random Walk in
American Lobster (*Homarus americanus*)**

Abstract

We tested the hypotheses that American lobster (*Homarus americanus*) movement is influenced by sex, density, days at large and season. We also explored the degree to which movements were best described as a diffusion process or as a directed migration. Lobster (n = 4 030) captured by experimental trap and trawl surveys over two years (May-July, October, 2001, 2002) were tagged and released in Northumberland Strait, eastern Canada. Recaptured lobster (n = 392) were caught and reported by commercial fishermen up to three years after the initial tagging experiment. The maximum and median distances were 58.3 and 8.7 km, respectively. Displacement per day was negatively correlated with density. Females moved farther than males in early summer. The sex-biased movement may be associated with female mate choice and male territorial behaviour. There was no directional bias in the movement of lobster released in July and August. Diffusion models fit to the density-distance distributions of tagged individuals at large for 1, 2, 3, and 4 weeks suggest a correlated random walk. I suggest that diffusion models offer a promising approach to distinguishing the behavioural heterogeneity and physio-geographic mechanisms of population redistribution.

Introduction

Individual lifetime net displacement, or dispersal, can result from large-scale movements that are random with respect to space, errors in directed to- and fro-seasonal migrations (Grinnell 1922, Quinn and Brodeur 1991), or from an accumulation of small-scale movements attributable to behaviours associated with foraging, mating and predator avoidance (Dingle 1996). At the population level, dispersal defines populations and

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metapopulations (Dobzhansky and Wright 1943, Pulliam 1988, Lebreton et al. 1992, Watkinson and Sutherland 1995, Caudill 2003), enables range expansion (Skellam 1951, Kot et al. 1996, Clark et al. 1998, Clark et al. 1999), and contributes to population persistence in temporally variable environments (Roff 1975, 1986, 1994).

Individual and mass mark-recapture studies are commonly used to study animal movement and population redistribution. Although both empirical and theoretical models of the density-distance distributions are used to extrapolate population redistribution from individual movement data (Kot et al. 1996, Turchin 1998, Clark et al. 1999), theoretical models such as diffusion and competition models have the potential to provide a more meaningful basis for understanding the mechanisms responsible for patterns of population redistribution (Turchin 1998). Random walk or diffusion models have been employed to describe the movement of many organisms including fruit flies, *Drosophila pseudoobscura*, (Dobzhansky and Wright 1943), muskrat, *Odatra zibethica*, (Skellam 1951), flea beetles, *Phillotreta cruciferae* and *P. striolata*, (Kareiva 1982) and several species of stream fish (Skalski and Gilliam 2000). The simplest of these models predicts a normal density-distance distribution. Deviations from the predicted normal distribution may indicate population and habitat heterogeneity (Dobzhansky and Wright 1943, Skalski and Gilliam 2000, 2003), and directional persistence, or a correlated random walk (Kareiva and Shigesada 1983, Turchin 1998).

The American lobster (*Homarus americanus*) is economically and socially important to Atlantic Canada. Facilitated by an intense commercial fishery, large body size, and ease of handling, mark/recapture tagging studies have often been used to quantify exploitation rate, growth and movement in this species (reviewed by Krouse

1980, Stasko 1980, Haakonsen and Anoruo 1994, Comeau and Savoie 2002). These studies have generally found that adult lobster can be highly mobile. Displacements of more than 1 km/day are not uncommon and yet, mean and median displacements over months and years are often less than 5 km.

Lobster exhibit a variety of individual movement behaviours and patterns. Movements that maintain a single or multiple dens, or depressions in close proximity to one another, are described as being characteristics of resident behaviour, while movements that do not contribute to the maintenance of a home range are described as being transient or nomadic (Lund et al. 1973, Herrnkind 1980, Ennis 1984, Karnofsky et al. 1989a, 1989b). Individuals may alternate between resident and transient behaviour throughout the warmer summer months, but are generally less active, and hence more resident, during colder winter months (Ennis 1984, Watson et al. 1999). Seasonal inshore-offshore movement (Bergeron 1967, Munro and Therriault 1983, Howell et al. 1999, Campbell 1986, Pezzack and Duggan 1986, Roddick and Miller 1992) may also be associated with migration behaviour, defined as persistent directed movement and the suppression of resident behaviour (Kennedy 1961).

Population heterogeneity in movement behaviour is often linked to size, sex, and maturity, reflecting the different life-history trade-offs. As lobster grow they become increasingly more mobile (review by Lawton and Lavalli 1995). Mature lobster moved farther than immature lobster in a tagging study off of New Brunswick (Campbell 1990), but most tagging studies in the Gulf of St. Lawrence do not show strong evidence of size-bias (Comeau and Savoie 2002), probably because of size-selectivity of the commercial fishery (in this study 55-122 mm Carapace Length). Sex-biased dispersal in both birds

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and small mammals has been linked to nesting behaviour and mating strategies (Greenwood 1980, Clarke et al. 1997). While mark-recapture tagging studies commonly find no difference in movement between the sexes in fish, in two species of marine fish (lingcod, *Ophiodon elongatus*: Smith et al. 1990, rig, *Mustelus lenticulus*: Francis 1988 in Attwood and Bennett 1994) females disperse farther than males, and in one population of brook trout, *Salvelinus frontinalis*, males disperse farther than females (Hutchings and Gerber 2002). Both male- and female-biased movement has been documented in tagging studies in the Gulf of St. Lawrence (Comeau and Savoie 2002).

The Northumberland Strait, a shallow strait on the southern edge of the southern Gulf of St. Lawrence (sGSL), is divided into two lobster fishing areas (LFAs), 25 and 26A (Fig. 1). LFA 25 has the only late-summer or fall fishery in the sGSL. The fall fishery was established, in part, in response to the assertion that the lobster fishery depended on a seasonal migration of lobster into the strait. However, tagging studies have provided little or no evidence of directed movements (Comeau and Savoie 2002). Rather, seasonal increases in catch rates, and differences in size composition of the commercial catch, have been attributed to increased feeding activity of post-moult lobster associated with the warmer waters of the strait (Templeman 1936, Wilder 1963, Comeau and Savoie 2002). Evidence for a lack of seasonal migration is, nonetheless, equivocal. Many of the previous tagging studies were based on single, usually post-fishery, release periods and dependent on recaptures by the fishery one year later (Comeau and Savoie 2002), such an experimental protocol that would have limited, if any, power to detect seasonal inshore-offshore movements by lobster.

Our objectives were three-fold: 1) to quantify lobster movement in LFA 25 by releasing tagged lobster in the spring, summer and fall to be recaptured by the commercial fishery in August through October; 2) to describe lobster movement with diffusion models; 3) to test whether individual lobster movement is related to size or sex.

Methods

Study Area

The focal area for the present study was Lobster Fishing Area (LFA) 25 in the Northumberland Strait (Fig. 3.1). The Northumberland Strait separates Prince Edward Island (PEI) from New Brunswick (NB) and mainland Nova Scotia (NS). It is approximately 320 km long and between 13 and 48 km wide. Water flows from west to east. The net flow is on the order of centimeters per day, while the tidal currents are an order of magnitude stronger (Joël Chassé, pers. comm.). Tides inside the strait are semi-diurnal, with a maximum tidal range of 2 m (Davis and Browne 1996). During summer, bottom water temperatures can approach 20 °C inside the strait. In winter, ice covers much of the strait and ice scour can affect the benthic community (Davis and Browne 1996).

In Canada, the lobster fishery is regulated by effort control and restrictions on the size and condition of landed lobster. In 2001, there were 793 license holders in LFA 25 (Comeau et al. 2004). Each license holder was allowed to fish 250 traps. Egg-bearing female lobster were prohibited from the landings and the minimum legal carapace length of lobster landed was 67.5 mm. LFA 25 has a fall (August-October) fishery while all

other LFAs in the southern GSL (LFA 23, 24, 26A and 26B) have spring (May-June) fisheries. Also, unlike the other lobster fisheries, the lobster fishery in LFA 25 is highly mobile; most fishermen set one or two traps per buoy and it is not unusual for them to move their traps throughout the LFA.

Mark/Release

In 2001 and 2002, a total of 4 030 lobster were tagged with streamer tags inserted into the dorsal musculature between the carapace and tail. Lobster were caught by experimental trapping in the spring and early summer, and by the Department of Fisheries and Oceans, Canada, (DFO) trawl survey in May, July, August and October in the Northumberland Strait (Fig. 3.1). The carapace length (CL) of lobster was measured from the eye socket to the end of the cephalothorax in a line parallel to the mid-dorsal line. Hardness of the shell behind the rostrum, to the left and right of the mid-dorsal line and at the lower edge of the cephalothorax was noted as being either soft or hard. Missing or regenerating chelae were noted and the sex, absence or presence of eggs and stage of eggs, when present, were also recorded.

Trawl Survey

DFO conducted a trawl survey to monitor the fishery in the Northumberland Strait between 2000 and 2003 (Comeau et al. 2004). Trawl stations were established on a 3.1 km (2 nautical miles) grid of all bottom deeper than 5 m and suitable for trawl gear. A No. 286 trawl with rockhopper footgear was towed for 15 minutes at 4.6 km (25 nautical

miles) per hour at stations chosen randomly in five strata defined by bottom type. The net had a 17.7 m (58 ft) head rope and a 21.9 m (72 ft) ground rope. Owing to weather and time constraints, the May and October surveys focused on the central part of LFA 25, between West Point and Confederation Bridge, while the July and August surveys encompassed all of LFA 25 (Fig. 3.1; see Comeau et al. (2004) for further details). During the trawl surveys, tagged lobster were usually held on board for 15 minutes and occasionally for extended periods to accommodate the trawl fishing. Tags were removed from lobster that were not responsive prior to release (roughly 2% of lobster).

Trap Survey

Five commercial fishermen completed the experimental trapping in Richibucto and in the central part of the strait in 2001 and 2002 (Fig. 3.2). The design and deployment of experimental traps varied among fishermen (Chapter 2), but all had blocked escape vents to enhance the catch of smaller lobster.

Tag Recaptures and Reports

In both 2001 and 2002, fishermen were mailed information about the tagging study prior to the start of the fishing season. The Maritimes Fishermen's Union's (MFU) wharf representatives, Department of Fisheries Oceans (DFO) biologists, and province of Prince Edward Island biologists also helped by collecting tag returns and posting information about the research project. The MFU and Prince Edward Island Fishermen's Association published articles on the research in their newsletters, and DFO maintained a

toll-free number to receive tag reports. In the fall of 2001, a public service commission

strike left the phones unattended and some tag reports were not received. In 2002,

fishermen were sent a tally sheet for recording information on tagged lobster with the

lobster licence and I visited all 30 wharfs at least once during the fishing season. In

addition, in 2002, DFO offered two prizes of hand-held GPS units (approximate value of

$400) to promote tag reporting.

Statistical Analyses

Statistical analyses were done with S-plus Professional Edition 6.1.2. Paired and

unpaired t-tests were used to compare mean displacement distances. Kolmogorov-

Smirnov tests were used to compare the size distributions of lobster tagged and released

by trap and trawl and recaptured by the fishery, and to compare the density-distance

distributions for lobster recaptured in 2001 and 2002. A Chi-square contingency test was

used to compare the ratio of male to female lobster released and recaptured. Generalized

linear models were fit to lobster displacements (Gaussian distribution) as a function of

days at large, carapace length and distance between capture and release with tags and

lobster density at time of release.

Circular Statistics

A Raleigh test of the mean vector, r, where

$$r = 1 / n \times [(\textstyle\sum \cos \theta)^2 + (\textstyle\sum \sin \theta)^2)]^{1/2},$$

was used to test for random and non-random distribution of directions (Batschelet 1981) of displacement between capture and release with tags and release with tags and recapture. A Raleigh test was also used to test for a paired correlation between the angle of displacement between the direction of displacement between capture and release (β) and between release and recapture (θ). The maximum r of the positive and negative angular differences ($\delta+ = \beta - \theta$, $\delta- = \beta + \theta$) was used as the test statistic. The absolute angular difference between lobster movement between release and recapture and the homeward direction (the displacement between capture and release) was calculated for all lobster, and the Wilcoxon-Mann-Whitney univariate rank test was used to compare homing ability of males and females. A rank-sum normal approximation with correction (z) was used for the test statistic when sample sizes were greater than 49 (S-plus Professional Edition 6.1.2). Hotellings 95% confidence elipses describe the bivariate displacement of lobster between release and recapture (Batschelet 1981).

Diffusion Model

A two-dimensional diffusion model (Turchin 1998), with infinite boundaries and point release, was fit to the density-distance distribution of lobster at large for 1, 2, 3 and 4 weeks. The local minimum for

$$N \text{ (per cent)} = N_o / (2 \times \pi \times D \times t)^{1/2} \exp (-x^2 / 4 \times D \times t)^2 ,$$

where, N was the number of lobster caught at a given distance, x, t was the number of days at large (t=7, 14, 21 and 28), N_o was the initial number of animals released, and D

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was the diffusion coefficient. N_o and D were fit to the observed distribution of captures using a general quasi-Newton optimizer (S-plus Professional Edition 6.1.2).

Results

Approximately 200 commercial fishermen in LFA 25 reported the tag number, date and location (GPS or LoranC coordinates) of the capture of tagged lobster. Eleven per cent of lobster released prior to the 2002 lobster fishery were recaptured and reported. Significantly more tagged lobster released one year or less prior to the fishery were reported in 2002 than in 2001 (Releases: reports in 2001: 129/1686 or 7%; in 2002: 211/2003 or 12%, χ^2 =7.2669, p=0.007). The number of reports of tagged lobster in each district in 2002 was positively correlated to the lobster landings in 2001 (Fig. 3.3). In both 2001 and 2002, reports per landing in 2001 were highest in the central part of the strait (districts 77, 78, 80 and 83).

The likelihood of recapture and reporting was the same for both males and females (M:F release 1908:2121, return 204:203, χ^2=1.0258, p=0.3111). Although there was no difference (ks=0.0721, p=0.1189) in the size distribution at the time of release between lobster tagged during the trap survey (n=753, mean=74.35, range=53-141) and those reported by the fishery (n=405, mean=75.98, range=55-122), the size selectivity of the fishery was significantly different (ks=0.1842, p<0.001) from that of the trawl survey (n=3 272, mean=75.45, range=43-153).

The displacement distances between release and recapture locations could be calculated for 390 tag reports. Two reports were discarded because the recapture

positions were in error: the positions reported were outside of LFA 25 in an area that was not open to fishing at that time. Seven small (65–77 mm CL) female lobster were released by fishermen and reported a second time; one was reported a third time (Fig. 3.4). The recapture of two tagged lobster was reported in 2003 and 2004 (displacement 33.62 km, 33.25 km). Both were females with eggs at time of release in July and May 2002, respectively.

Fifty percent of the lobster tagged and released in the Northumberland Strait moved less than 8.69 km (Table 3.1). The largest displacement of lobster was 58.26 km, the mean displacement was 12.24 km. There was no difference between the distribution of displacements of lobster released and recaptured in 2001 and 2002 (2001: n=129, mean =13.47, range =0.27-58.26; 2002: n=232, mean =11.30, range=0.33-53.38; ks=0.1203, p = 0.1571). Although displacements of up to 40 km occurred between capture and release with tags during the trawl survey, the displacement between capture and release with tags was not correlated to the displacement between release and recapture (Fig. 3.5A). Displacement between release and recapture was also not correlated with the size of lobster at the time of release (Fig. 3.5B).

There was no significant difference between the displacements of lobster in October (n=6, mean=15.98, range= 1.91-36.81) and May and June (n=17, mean=22.34, range=0.48-58.26; t=0.8372, df=21, p=0.4119; ks=0.3725, p=0.4499, Table 3.1). However, the displacement of lobster released in July, August and September (n=363, mean=11.70, range=0.27-53.38) was less (t=3.9127, df=384, p=0.0001; ks=0.2842, p=0.0504) than that of lobster released in October, May and June (n=23, mean=20.68, range=0.48-58.26). The displacement of lobster per day at large was also greatest for

lobster released in July and August. For lobster at large for less than one month (31 days), the number of days released was positively correlated to the distance traveled (Fig. 3.6). The relationship between displacement distance and time at large was not significant for lobster at large for more than 31 days. Lobster displacement between release and recapture was negatively related to the density of lobster at the time of release (Fig. 3.7). Further, the density at time of release was still significantly related to the displacement in a model that included the days at large, which is an indication of fishing effort (Table 3.2).

There was a sex bias in displacement distance; female lobster (n=192, mean=13.89, range=0.31-58.26) moved farther (t = -2.7763, df = 381, p=0.0058) than males (n=191, mean=10.82, range=0.27-42.46). For lobster at large for less than 31 days, the displacement per day was significantly (t=-1.992, df=230, p=0.0475; ks=0.2214, p=0.005) higher for females (n=112, mean=0.88, range=0.01-12.11) than for males (n=120, mean=0.57, range=0.01-7.11).

Raleigh tests showed no directional bias in the displacement of lobster between release and recapture for either males (n=155, r=0.0616, p = 0.5553) or females (n=155, r=0.0291, p=0.8774). Hotelling's 95% confidence intervals on the displacement of lobster encompassed the origin for both males and females released during the summer, but for those lobster released during October, May and June movement was biased to the northwest (Fig. 3.8). The diffusion coefficients of random walk models fitted to the displacements of lobster at large for 1, 2, 3 and 4 weeks increased with number of weeks at large (Fig. 3.9).

There was a positive correlation between the direction of displacement between capture and release with tags (β) and between release and recapture (θ) for both males (n=155, r+=0.1865, p=0.0046) and females (n=155, r+=0.1444, p=0.0394), but the assumption of random independent samples was violated for females; the distribution of angles of displacement between capture and release with tags was non-random for females (n=155, r=0.1799, p = 0.0066) but random for males (n=155, r=0.0699, p=0.4686). A Wilcox rank-sum test of dispersion was used to compare the rank of the absolute angular difference between the homeward direction (opposite of the displacement between capture and release) and the direction of movement between release and recapture between males and females. Males had a marginally stronger homing tendency than females (all reports: n males=155, n females=155, z=-1.9155, p=0.0554; at large for 31 days or less: n males=99, n females =95, z=-1.687, p=0.0916; at large for 7 days or less: n males= 13, n females=11,W=127, p=0.041).

Discussion

The Northumberland Strait is a wide shallow strait with a relatively homogeneous bottom that may facilitate the movement of lobster (Templeman 1936, Comeau and Savoie 2002). The mean and median displacements observed in the present study, as with earlier studies, are greater than observed elsewhere in the Gulf of St. Lawrence (Comeau and Savoie 2002). There is no evidence in these earlier studies or the present study of directed movement of lobster into the Northumberland Strait during the summer (Fig. 3.8B). In contrast, displacement of lobster released in May and June (Fig. 3.8A) were biased towards the northwest or out of the strait. While displacement to the

northwest for individuals released in October (Fig. 3.8C) is consistent with the hypothesis that lobster exhibit an outward migration, observation bias resulting from the limited release area relative to the distribution of the fishery, may also account for the northwest bias of lobster released in May, June and October (Fig. 3.8A and C).

Observed displacements are a function of lobster movement, and the distribution of releases, fishing effort and the likelihood of reporting. Fishermen in LFA 25 do not have to report where they fish, but the distribution of fishing effort might be expected to reflect the distribution of lobster (Campbell 1986, Swain and Wade 2003), particularly in this LFA, where the fishermen do not have traditional fishing areas or berths and fish throughout the LFA. The DFO trawl survey shows high densities of canner- (> 67.5 and < 80 mm CL) and market- (> 80 mm CL) size lobster near West Point, PEI (Comeau et al. 2004), northwest of the majority of release sites in May, June, and October.

More lobster recaptures were reported in 2002 than 2001 (Fig. 3.3), possibly because of increased awareness of the project, the tally sheets, and the GPS prizes. The number of recaptures reported in a statistical district was correlated to the landings (Fig. 3.3), but in the central strait (districts 77, 78, 80 and 83), the number of tag reports was under-predicted by the landings. There may have been greater reporting by the fishermen in these districts because this was the focal area for this research project and there had been a decline in commercial landings (Comeau et al. 2004).

Lobster released in July and August moved less than lobster released in the fall and the spring, but the movement was positively correlated to time at large (Fig. 3.6), suggesting that captured animals would have continued to move if they had remained at large. Yet, there was no difference between the displacement of lobster released in the

fall and in the spring. Although samples sizes were small, this result suggests limited movement of lobster during the winter months. The diffusion coefficient or mobility of lobster increases with the number of weeks at large (Fig. 3.9), suggesting a correlated random walk. A correlated random walk differs from a random walk in that turning angles of individuals are biased resulting in directionally persistent movement.

The appropriate scale to study lobster movement may vary seasonally and between locations. Watson et al. (1999) tracked 26 lobster with acoustic tags in New Hampshire and documented sporadic movement with 2 to 4 weeks of residential behaviour followed by short bursts of movement which covered several kilometres. The net result of these movement behaviours resulted in movement into or up the bay in the spring and outward movement in the fall. While, the high maximum rates of movement with very short release periods is consistent with bursts of movement or tag-induced nomadism, the increase in the diffusion coefficient with days at large suggests the latter.

Lawton and Lavalli (1995) describe ontogenetic changes in lobster behaviour from shelter-restricted post-larvae to increasingly vagile juveniles and mature lobster are more mobile than immature lobster (Campbell and Stasko 1985 and 1986, Campbell 198). However, we find no effect of body size on the displacement of lobster (Fig. 3.5B). The size composition of lobster in opportunistic mark/recapture fisheries is limited to the sizes that are caught in the fishery (55-122 mm CL). The lack of a size-effect in the present and earlier studies in the sGSL (Comeau et al. 2002) may result from the size-selectivity of the fishery. In this opportunistic mark-recapture study there is also an insufficient range in the size of recaptured lobster to test the hypothesis that very large, possibly dominant, lobster are less likely to move than smaller lobster.

An ontogenetic shift from shallow to deeper waters has been documented in marine decapods (Pardieck et al. 1999, Childress and Herrnkind 2001). Lobster settle in high density and juvenile hotspots (Palma et al. 1999, Steneck and Wilson 2001) may set the stage for density-dependent dispersal, however we found a negative correlation between lobster density at the point of release and displacement (Fig. 3.7). One explanation for the negative relationship is that fishing effort may have been concentrated in areas of high lobster density, such that lobster in these areas would be more intensely fished and have less time at large, but displacement is negatively correlated to both datys at large and density at time of release (Table 3.2). The lobster population in the strait experiences a high fishing mortality (Chadwick 1998) such that densities may not be sufficient to elicit density-dependent dispersal. The maximum number of lobster per tow is roughly 0.66 lobster/m^2. Areas of high lobster density may also indicate preferred habitat, or may be associated with complex habitat in which the one-dimensional displacement distance may underestimate distance moved.

In the sGSL, most tagging studies have documented little difference between distances traversed by males and females, while others have found both male- and female-biased movement (Comeau and Savoie 2002). In the present study, female lobster moved farther than males, and with 31 days at large or less, females moved faster than males. On the Atlantic coast of Nova Scotia, female-biased movement appears to be associated with the maintenance of optimal temperatures for egg development (Campbell 1986), but in the present study there were very few egg-bearing females, and the difference between females without eggs at time of release and males is significant. Female-biased movement of lobster in the Northumberland Strait released in July and

August may be associated with mating behaviour. Male lobster are territorial and defend one or more dens, while females choose mates/dens (Atema et al. 1979) and hence may be more mobile than the males. We also find that males show a greater propensity to move in a direction toward point of initial capture or home than females, which may be associated with territorial behaviour. Further research with a more substantial sample size and better design is needed to test the hypothesis that males released prior or during the moulting will home.

While diffusion models are not widely used in fisheries to describe mark and recapture data (but see Attwood and Bennett 1994), they could be used to distinguish between differences in lobster behaviour and landscape or physio-geography. It has been argued that male-biased lobster dispersal in estuaries and bays (Bergeron 1967, Munro and Therriault 1983, Jury et al. 1994, Howell et al. 1999, Watson et al. 1999), results from greater physiological tolerance of male lobster to high temperatures and low salinities (Jury et al. 1994a, 1994b, Howell et al. 1999, Watson et al. 1999). Diffusion models could also be used to test the hypothesis that the greater mobility of lobster in Northumberland Strait results from the relatively flat area available for movement compared to the rest of the Gulf where the steeper coast descends to the unsuitable habitat of the cold intermediate layer (Templeman 1936, Comeau and Savoie 2002). A similar analysis could be extended to the Atlantic coastline where water is warmer at depth and suitable lobster habitat extends to the continental shelf.

Few researchers attempt to link individual movement to population redistribution (Turchin 1998), which is a function of the initial population distribution, life history, and habitat landscape. Basic distribution and abundance data are missing for American

lobster (Steneck and Wilson 2001), and this seriously compromises movement studies.

Also, despite the recognized importance of observation bias (Bumpus 1901 cited in

Lawton and Lavalli 1995, Barrowclough 1978, van Noordwijk 1984, Stenseth and

Lidicker 1992, Porter and Dooley 1993, Turchin 1998, Hilborn 1990, Baker et al. 1995,

Koenig et al. 1996, Whitehead 2001, Albanese et al. 2003), the absence of information on

the spatial distribution of recapture or fishing effort further undermines mark/recapture

studies. Nonetheless, diffusion models are a useful tool to predict population

redistribution and explore mechanisms. This conceptual framework encourages

thoughtful experimental design that considers assumptions and biases, such as the initial

population distribution and the distribution of release and recapture effort.

Fishermen's Association and the province of Prince Edward Island Department of

Fisheries, Aquaculture and Environment helped collect tag reports from fishermen.

Table 3.1. Summary of data on displacement of lobster released in 2001 and 2002 and recaptured and reported in 2001 (n=134), 2002 (n=252), 2003 (n=1) and 2004 (n=1).

Month Released	Number Released[1]	Number Recaptured	Median Distance (km)	Mean Distance (km)	Standard Error	Minimum Distance (km)	Maximum Distance (km)
May	170	9	16.29	20.84	6.34	0.49	58.26
June	71	8	24.32	24.07	5.08	5.71	48.90
July	2 496	272	10.38	13.66	0.64	0.27	53.38
August	746	91	3.61	5.82	0.71	0.47	43.97
September	0	1	2.72	2.72	-	2.72	2.72
October	547	6	9.78	15.98	5.78	1.91	36.81
Total	4 030	388	8.69	12.24	0.55	0.27	58.26

[1] The number of released lobster reported here are only those released at the time of tagging. There were at least 9 tagged lobster captured and released by fishermen during the fishery in August, September and October.

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Table 3.2. Summary of the linear model of displacement between release and recapture predicted from days at large and the logarithm of density of lobster at the time of release (number of lobster per km towed). N=239, r^2=0.1171, p<0.001.

	Value	SE	T value	p-value
Intercept	16.1731	1.5798	10.2377	<0.001
Days at large	0.0164	0.0053	3.1116	0.0021
Log10 density at release	-5.3424	1.1546	-4.6270	<0.001
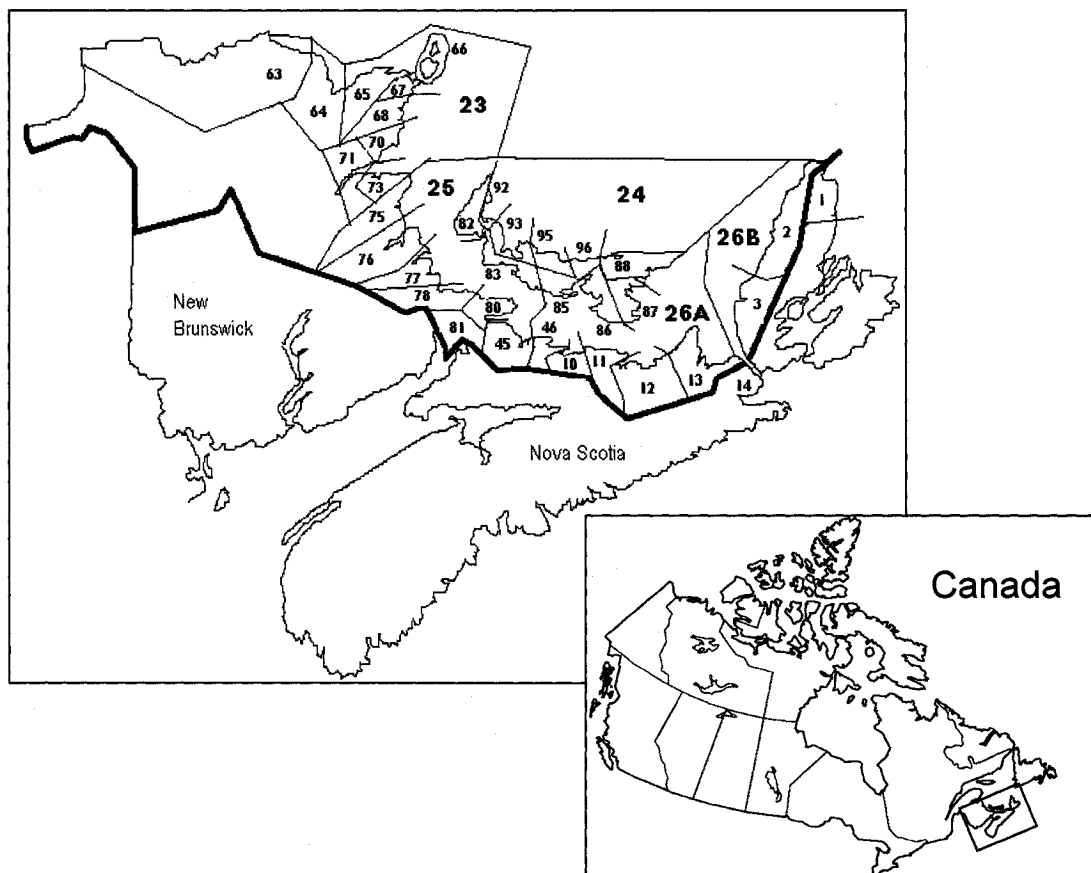
Fig. 3.1. Map of the Fisheries and Oceans Canada (DFO) lobster fishing areas (LFAs) and statistical districts in the southern Gulf of St. Lawrence.
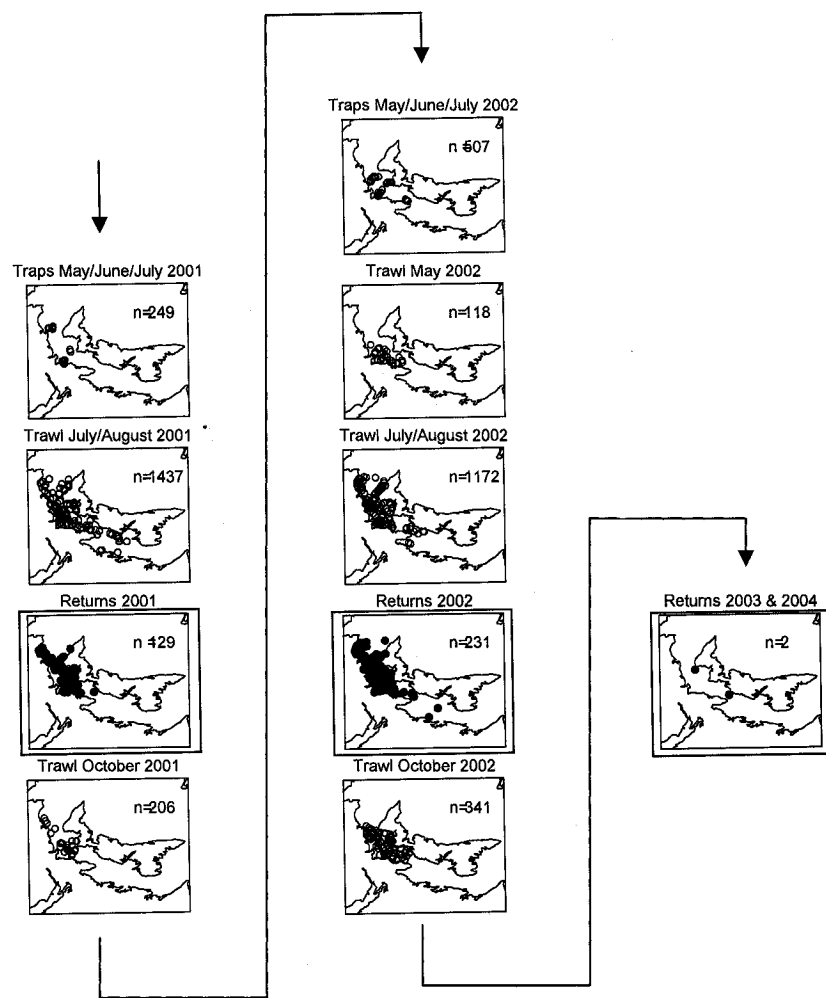
Fig. 3.2. Distribution of release sites for lobster tagged in 2001 and 2002 and recaptures reported during the fall fishery in LFA 25 in 2001, 2002, 2003 and 2004. The maps of recapture locations are indicated by the double boxes.

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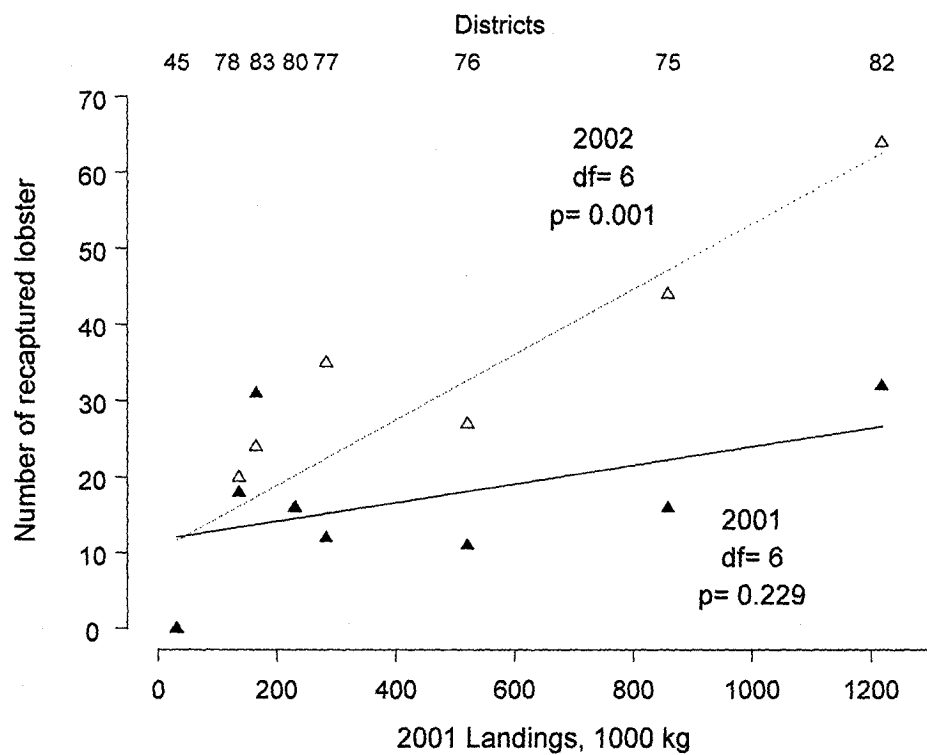
Fig. 3.3. Plot of landings and reports of recaptured tagged lobster by statistical district in LFA 25 (Fig. 1). The statistical districts are identified across the top, and open triangles are 2002 and closed triangles are 2001. There are two data points hidden.

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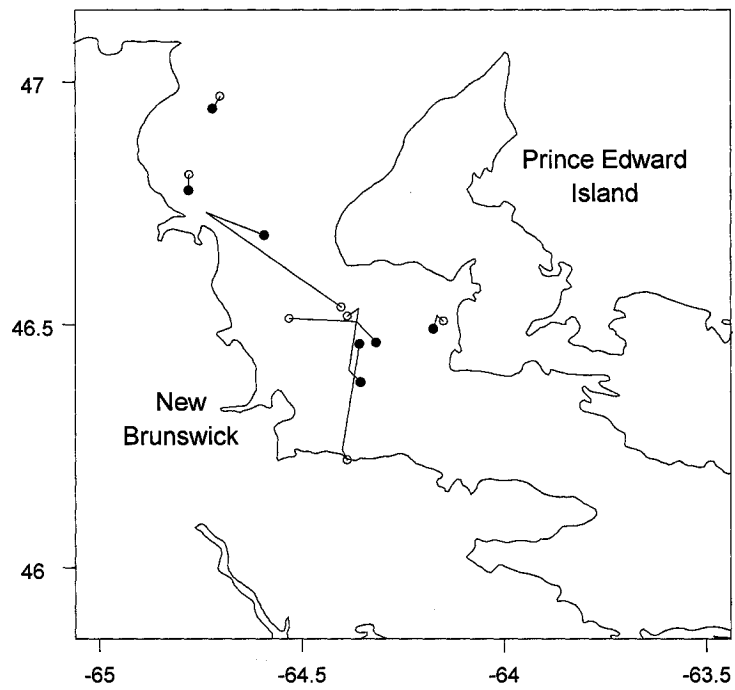
Fig. 3.4. Tracks of seven female lobster (65-77 mm CL) caught twice and one lobster caught three times. The closed circle indicates the initial release point and the solid circle for last reported capture site.

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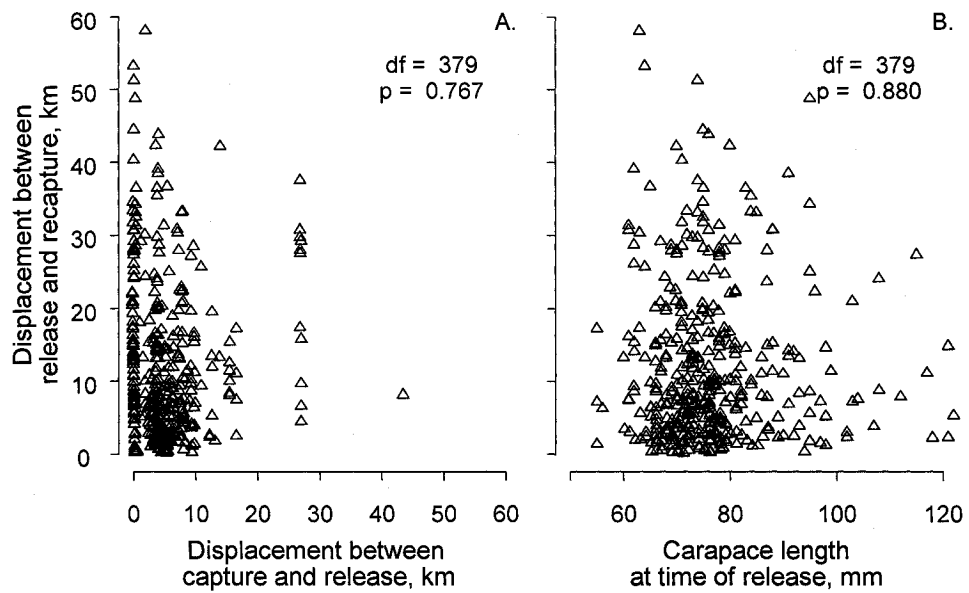
Fig. 3.5. Displacement between release and recapture vs. displacement between capture and release with tags (A) and the size of lobster at the time of release (B).
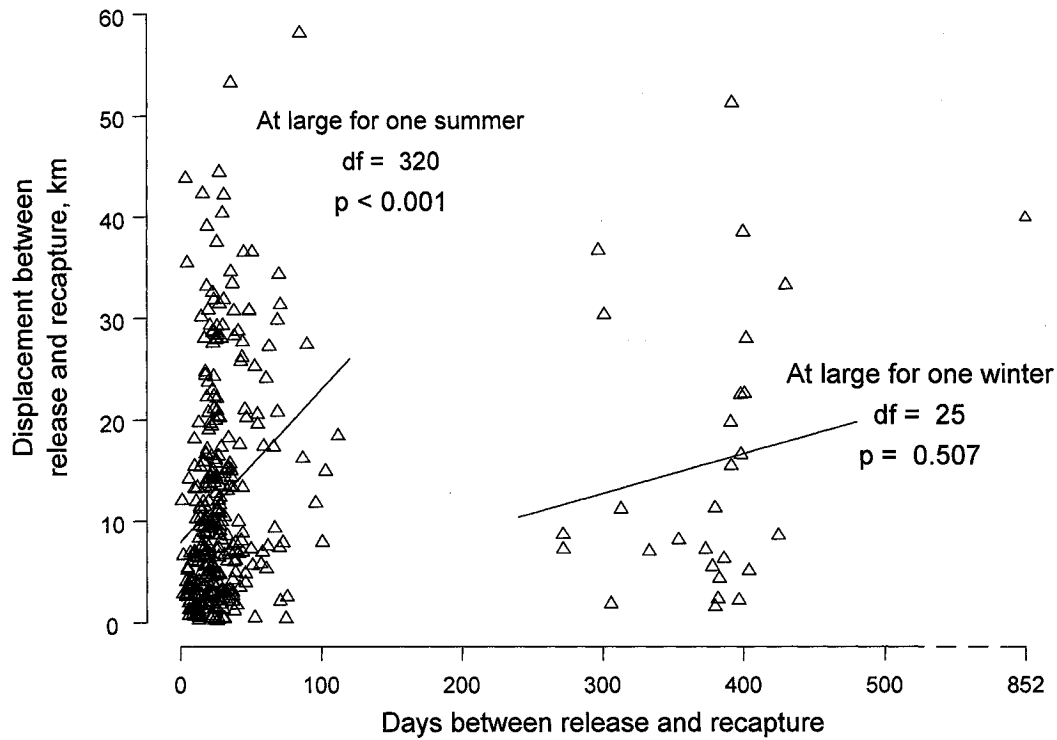
Fig. 3.6. Plot of the days between release and recapture and the displacement between release and recapture. The lines were fit assuming a normal distribution of displacements. Thirty-seven displacements are missing because the recapture date was not reported.
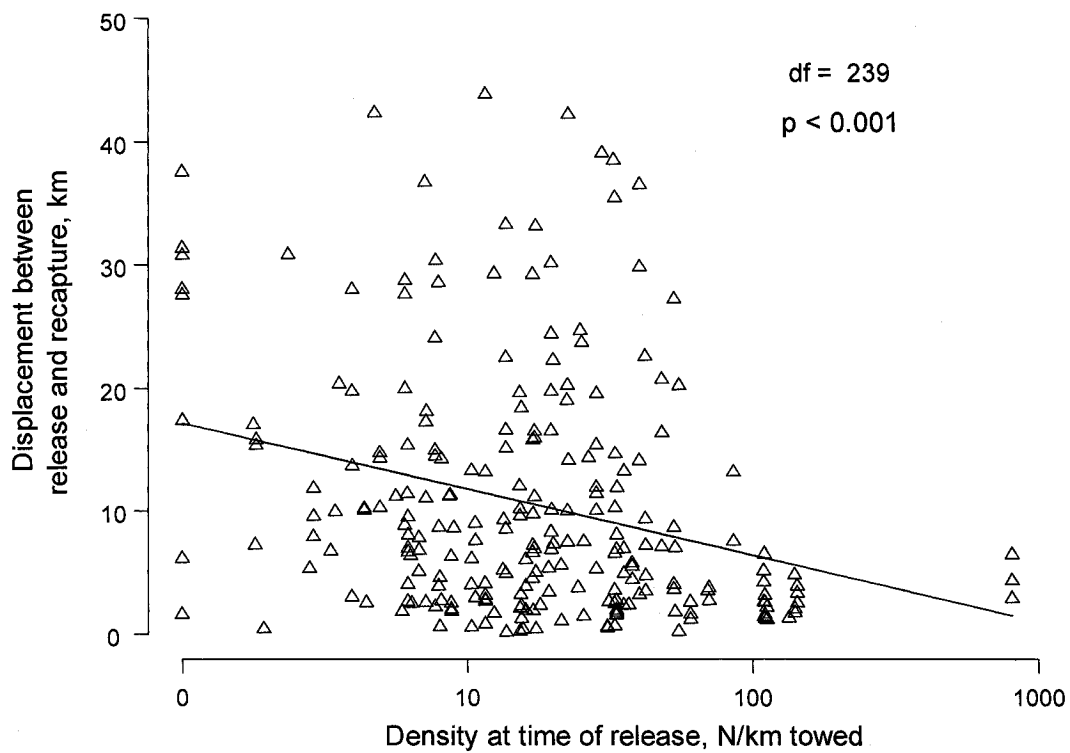
Fig. 3.7. Displacement between release and recapture vs. the number of lobster per km of trawl towed on a logarithmic scale. The predicted line (y=17.21-5.41x) was fit (n=240, r^2=0.0812, p<0.001) assuming a normal distribution of displacements.
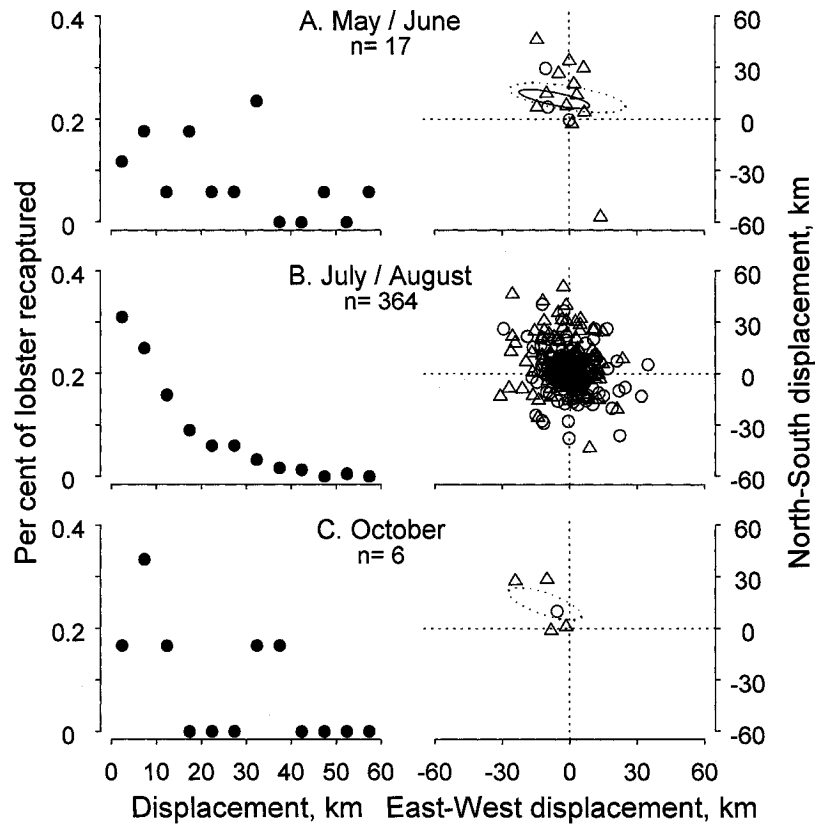
Fig. 3.8. On the left, plots of percent of lobster recaptured by distance traveled (km) for each release period. On the right, net displacement (km) of individuals between the point of release (the origin) and the point of release for each release period. The open triangles are males and the circles are females. Hotellings 95% confidence intervals are fit to the bivariate positions and encompass the origin for July / August releases (B) but are displaced to the north-west for lobster released in October (C) and May / June (A). (The single recaptured lobster released in September is not presented.)

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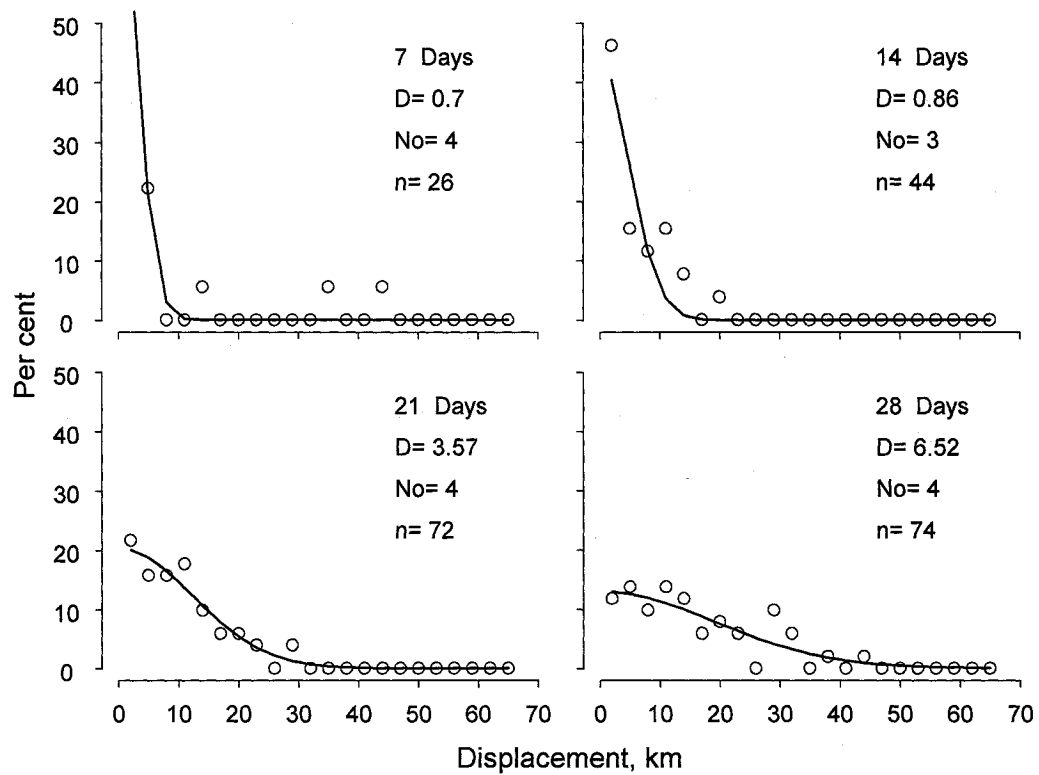
Fig. 3.9. Diffusion models fit to the density-distance distributions of lobster at large for 1, 2, 3 and 4 weeks. The diffusion coefficient (D) and the initial population size (No) were estimated from the data using the nlmin function of S-plus Professional Edition 6.1.2.

CHAPTER 4

Small-Scale Movements of American Lobster (*Homarus americanus*)
in a Shallow Strait Identified by
Radio-Acoustic Positioning and Telemetry (RAPT)

Abstract

Small-scale movement of lobster (*Homarus americanus*) was tracked with radio-acoustic positioning and telemetry (RAPT) in the Northumberland Strait, Canada, in July 2001. Acoustic tags were attached to eight lobster (81-114 mm Carapace Length). Three lobster remained in the hydrophone array for the duration of the study month of July, four lobster moved less than 2/3 km outside of the hydrophone array after two weeks at large, and one lobster left the study area. For the three lobster that stayed in the hydrophone array the home ranges, described by the Minimum Convex Polygon (MCP) of all positions during July, were 240.39, 564.77 and 1501.31 m^2. Activity, measured by the displacement between successive positions and total area covered, varied among individuals and between days. There was no difference in lobster activity during the day and night. Because of the very limited movement of resident lobster in the central part of the Northumberland Strait during the month of July, these lobster are ideal for tracking with the RAPT system. However, the movement of the hydrophone buoys biases the triangulated positions, and modifications to the system to either fix the buoys, or track or model hydrophone buoy positions is necessary to track small-scale lobster movement over extended periods of time.

Introduction

The maintenance of a home range and/or dens, nests or shelters may be important in avoiding predators, foraging, mating and establishing a social structure. Small-scale movements define home ranges, habitat use and have been used as an indication of activity in both marine fish (Bradbury et al. 1995, Connolly et al. 2002) and decapods

(Hines et al. 1995, Jernakoff et al. 1987, Smith et al. 1999). Studies of small-scale movement behaviour can also describe behaviour around traps for commercial species such as lobster (Jernakoff et al. 1988, Tremblay et al. 2003), crab (*Cancer pagurus*, Skajaa et al. 1998), and ling (*Molva molva*, Løkkeborg et al. 2000).

Direct observation of animal tracks can be made for very few species. Recent technological advances provide continuous and real-time tracking in a variety of environments, making it possible to study cryptic, long-lived, and highly mobile animals. Remote tracking can also reduce interaction with observers and consequently provide tracks that better represent natural behaviour. Lobster have been used as model organisms for the development of underwater telemetry arrays because they are large in size, have an external carapace and, as benthic invertebrates, move primarily in two dimensions (Lund 1970, Herrnkind 1980, Phillips et al. 1984, O'Dor and Webber 1991, Freire and González-Gurriarán 1998, Smith et al. 1998). Individual lobster movement has also been tracked over larger distances and longer time periods with acoustic tags and mobile hydrophones (Lund et al. 1973, Herrnkind 1980, Maynard and Conan 1984, Jarvis 1989, Watson et al. 1999). Recently, a large acoustic array was deployed in the Northumberland Strait to study large-scale lobster movement, without the bias associated with the distribution of opportunistic mark-recapture (Bowlby 2006).

Adult lobster exhibit a variety of movement behaviours, commonly described as resident (or territorial or central place foraging) and transient (Lund et al. 1973, Ennis 1984, Karnofsky et al. 1989a), roaming and resting (Maynard and Conan 1984), or homing, nomadism, and migration (Herrnkind 1980). Individual American lobster may alternate between these movement patterns over days and weeks and are more likely to be

resident in the winter than in the summer (Ennis 1984, Watson et al. 1999). Lobster, like other decapods, are generally active at night or dusk (Ennis 1984, Karnofsky and Price 1995, Smith et al. 1999, Tremblay et al. 2003). However, in areas where tidal currents are strong, or during winter months when daily variation in light levels may be limited, activity may not show a strict diel cycle (Jarvis 1989, Smith et al. 1999).

This pilot project was designed to assess the feasibility of using radio-acoustic positioning telemetry (RAPT) system on lobster in the Northumberland Strait. The study assesses the potential for using RAPT to track lobster in the Northumberland Strait, given the physical oceanography of the area, the limitations of the hydrophone buoy array, and the behaviour of lobster. The study is part of a larger one investigating the migratory behaviour of lobster in the Northumberland Strait, and provides the first high resolution (10 m, <10 min) tracks of small-scale lobster movement in this area.

Methods

Study Area

The Northumberland Strait separates Prince Edward Island from New Brunswick and Nova Scotia on the southern edge of the Gulf of St. Lawrence, Canada (Fig. 4.1). It is roughly 320 km long and between 13 and 48 km wide. Water flows from west to east. The net flow is on the order of centimeters per day, while the tidal currents are an order of magnitude stronger (Joël Chassé, personal communication). Tides inside the strait are mixed or diurnal with a maximum 2 m tidal range (Davis and Browne 1996). In July and August bottom water temperatures can be as high as 20 °C. The sediments of the

Northumberland Strait are composed of tills, relict gravels, sands and silts (Davis and Browne 1996).

In the weeks preceding the RAPT study, 20 lobster traps were hauled every 2 to 4 days. Males and non-ovigerous females larger than 81 mm carapace length (CL) were selected. Because catch rates were low (less than 1 lobster per trap haul, see Chapter 2), lobster were held in the traps for up to 4 days prior to release with the acoustic tags (Table 4.1). Lobster carapace length (CL) was measured from the eye socket to the end of the cephalothorax in a line parallel to the mid-dorsal line (Chapter 3). Lobster were marked with a polyeurothane streamer tag sewn into the dorsal musculature between the carapace and tail.

Acoustic Tags

VEMCO® (Shad Bay, Nova Scotia, Canada) VR16 acoustic tags (length 58 mm, diameter 16mm, 51-78 kHz) were attached to a 2-3 cm^2 piece of inner tube rubber with monofilament line (Fig. 4.2). After drying the lobster carapace with acetone, 5 minute epoxy (Master Craft) was used to attach the foot to the surface of the lobster and to reinforce the attachment of the tag to the inner tube foot. Lobster were returned to the water from the boat near the center of the hydrophone array (Fig. 4.3) on July 1, 2001. Two VR16 acoustic tags were also attached to two unbaited lobster traps, which were deployed inside the hydrophone array.

Radio-Acoustic and Positioning Telemetry

The VEMCO RAPT system used for this study was comprised of 4 hydrophone buoys with radio transmitters and a receiver/base station (Fig. 4.3). Three hydrophone buoys were deployed in a triangular array of approximately 250 m sides just off of Pointe aux Bouleaux, New Brunswick (Fig. 4.1). The fourth hydrophone buoy was rotated into the array for battery recharging. The mooring line for the hydrophone buoys had a bungee cord insert (Ron O'Dor, personal communication) to minimize the movement of buoys in response to tide and currents.

The RAPT system is multiplexed, such that hydrophones listen in sequence for each of the tags and periodically signal each other to estimate distances between the buoys. The cycle length is a function of the number of frequencies detected and the amount of time allotted for detection. The median cycle length in this study was 6.4 minutes. The distances between the hydrophone buoys were calculated every hour. Replacement of hydrophones, thunder and lightening storms and data management resulted in several periods of 45 minutes or more for which there are no data.

The times at which acoustic signals were received by the hydrophones were transmitted by radio to the base station (Fig. 4.3). The base station provided real-time triangulated positions and saved the raw data. Post-analysis of the raw data included removal of extreme values and the calculation of positions from the intersection of the hyperbolae that describe the difference in the time of arrival of acoustic signals between two hydrophones (O'Dor et al. 1998).

On July 9, 2001, the hydrophone array was reduced and reoriented so that the focal acoustic tags attached to lobster were in the middle of the array, where error in the positions is the smallest (Tremblay et al. 2003).

Positions Outside of the Hydrophone Array

A mobile directional hydrophone was used to locate the acoustic tags that were outside of the hydrophone array on 6 days between July 4 and July 18 (Table 4.2). The lobster outside of the array were found in the same general area each time they were positioned, however the locations are only available on July 4, 5 and 18 (Fig. 4.1).

Triangulation

The calculation of the position of the acoustic tags from the hydrophone array incorporates the assumptions that: 1) the movement of the lobster is limited to one plane; 2) the speed of sound in water is constant; and 3) the hydrophones are fixed in position. Violations of the first two assumptions are not expected to have effected the positions as the slope of the bottom in the study area was gradual with the exception of a sandstone ridge less than 1 m high (personal observation), and while there was an increase in water temperature during the study period, within the array temperature would have been constant. However, the distance between the hydrophone buoys varied on a daily basis with wind and tide, and on a couple of occasions moorings were shifted either intentionally or during the replacement of hydrophone buoys for battery recharging. The

tag positions inside the hydrophone array were calculated from the mean buoy positions

in the four time periods in which the moorings positions were unchanged (Fig. 4.4).

Echo Filter

Errors in position can also result from echoes or reflections of the acoustic signals

such that the times of arrival at the hydrophones result in large displacements between

subsequent positions (Løkkeborg et al. 2000). All positions, for which net displacement

between subsequent moves was four times greater that than the gross displacement, were

deleted. Data were filtered once. This filtering removed 10-20 % of the positions for nine

of the acoustic tags, and 50% of the positions for lobster tag (LT) 3970 (Table 4.1).

Correction for Movement of Hydrophone Array

Movement of the hydrophone buoys with tide produced an elliptical track for both

traps and tags (Fig. 4.5) and oscillations in the positions in both the x- and y-direction

(Fig. 4.6). To correct the positions for the bias produced by the periodic movement of the

buoys, one of the two traps was used as a reference (TT 3812). The data were partitioned

into 14 time periods, within which neither the traps nor the hydrophone buoys were

repositioned. Corrected positions were estimated as the mean position plus the residual of

the correlation between the focal tag (attached to either the second trap or a lobster)

position predicted from the reference trap position (Table 4.3). Using this method to

correct from the movement of hydrophone buoys underestimates the extent of the

extreme positive and negative displacements, as the regression analysis used to correct

for the bias assumed no error in the position of the reference tag, which underestimates

the slope of the regression.

Statistical Analyses

R 2.1.1 was used for statistical analysis. Step lengths, during time periods of 20

minutes or less, were compared with t-tests to test for differences in mobility or activity.

The adehabitat 1.4 R-package (Clément Calenge, 2006/02/01) was used to determine the

Minimum Convex Polygons (MCP) to describe home range. The accuracy of the MCP

estimate of home range increases with sample size and is not biased by a lack of

independence of subsequent positions (Swihart and Slade 1985).

Results

Three lobster remained near the center of the array for the entire study period

(Fig. 4.5). Within the first day, two lobster moved outside of the range of the hydrophone

array. Three other lobster were detected by the hydrophones in the array, and were found

with the mobile hydrophone to be just outside the array (Fig. 4.5). The positions of one

of these lobster (LT 3970) were erratic and another (LT 3968) distinctly hyperbolic,

suggesting that the triangulated positions were unreliable. On July 18, seven of the eight

acoustic tagged lobster were within 0.66 km of the release point, four were located just

outside of the array (Fig. 4.2) and 3 inside the hydrophone array.

Even after filtering to remove possible echoes, there are more than 2500 positions

for each of the 3 lobster that stayed in the middle of the array, and more than 4000

positions for the trap (Table 4.2). The oscillations in the x- and y-displacements of the acoustic tags were large compared to the movement of lobster (Fig. 4.7), and more than 89% of the variation in the x- and y-displacements of the focal trap could be explained by the x- and y-displacement of the reference trap in all the time periods (Table 4.3). The correlations between the x- and y-displacements of the reference trap and the lobsters were weaker and more variable (r-squared=0.01% to 99%).

The lobster and focal tag positions from the first day of release were not corrected for bias produced by hydrophone buoy movement because there were no data from the reference trap (TT 3812) and one lobster (LT 3964) prior to day 2 (July 2, 2002). However, the net displacement of the lobster that left the array in the first day (LT 3962, LT 3968, LT 3969, LT 3970) was large relative to the bias produced by the movement of the buoys (Fig. 4.6). In the first day of release, the step lengths of less than 10 minutes were significantly larger (t=4.5824, p<0.001, df=89.974) for lobster (mean step length=5.07, n=86), than the tag affixed to the trap (mean step length=1.10, n=35). Further, the step lengths of the lobster that left the array (mean step length=14.72, n=23) were significantly greater (t=6.1575, p<0.001, df=22.222) the step length of the lobster (LT 3965 and LT 3966) that remained in the array (mean step length=1.54, n=63).

The variability in the corrected positions of the focal trap indicates the precision of this deployment of the RAPT telemetry system. Before the July 9, the 95% confidence intervals for the x- and y-displacement of the trap were +/-1.83 and 0.80 m. After July 9, the confidence intervals of the x- and y-displacements were +/-1.00, and 0.97 m, respectively (Table 4.4). The corrected x- and y-displacement was less for the focal trap than for the lobster (Fig. 4.7), the ground covered or displacement from the center of

activity was less for the focal trap (Fig. 4.8, 4.10), and the step lengths were smaller (t=43.6695, p<0.001, df=12275.24, lobster mean step length=1.57, n=9322, trap mean step length=0.73, n=3962), than for the lobster (Fig. 4.10A).

Activity Pattern

Although lobster movement was very limited, for each of the three lobster that remained in the array there were some days when they covered a greater area than the others (Table 4.4, Fig. 4.8). Overall, LT 3966 had the greatest step lengths (Fig. 4.10A) and covered the most ground on 15 of the 28 days of the study. There were, however, fewer positions for LT 3966 and the durations of the steps were more variable and significantly larger than those of the other two lobster (Fig. 4.10B, mean LT 3966=8.09, mean LT 3965=7.59, t=6.8217, df=4364.359, p<0.001; mean LT 3966=8.09, mean LT 3967=7.56, t=7.1644, df=4393.002, p<0.001) which are not significantly different from each other (mean LT 3965=7.59, mean LT 3967= 7.56, t=0.4164, df=7195.312, p=0.6772). There was no difference (t=-0.02383, df=9333.484, p=0.9774) between the step lengths during the day (between 7:00 and 21:00, mean step length=1.57 m, n=1503) and night (between 21:00 and 9:00, mean step length=1.57 m, n=6075, Fig. 4.11A). There was also no difference (t=-1.0429, df=2580.69, p=0.2971) between the step lengths between day (mean step length=2.83, n=1503) and night (mean step length=2.19, n=1350) for only the lobster that covered the most ground on any given day (Fig. 4.11B).

Discussion

There is considerable debate about the migration of lobster in the Northumberland Strait. While tagging studies have failed to demonstrate seasonal migration (Templeman 1936, Wilder 1963, Comeau and Savoie 2002, Chapter 3), changes in the abundance of lobster observed during other commercial fisheries, recreational diving, experimental trapping, and a DFO trawl survey suggest lobster migrate into the strait in mid to late July (Jamieson and Campbell 1985, Lanteigne et al. 2002, Chapter 2). The lobster tagged in the present study were captured in late June and early July and probably over-wintered in the area, possibly maintaining a shelter to avoid winter storms and ice scour. These resident or over-wintering lobster move very little in the month of July. Seven of the lobster released with acoustic tags were located within 2/3 km of the release point more than two weeks after release. And, three of these seven remained within the hydrophone array throughout the month of July. Only one lobster was not detected by the mobile hydrophone or the hydrophone array after the second day at large.

The larger step lengths of the lobster that left the array on the first day of release (Fig. 4.6) may be indicative of stress induced by tagging and release. Herrnkind (1980) suggested capture, handling and displacement during release could induce nomadic behavior in spiny lobster and bias tagging studies. However, Newland and Chapman (1993) found that acoustic tags slowed tail-flipping movement in the Norway lobster (*Nephrops norvegicus*), but had no effect on walking rate. Maynard and Conan (1984) observed no difference in the behaviour or survival of lobster tagged in the lab. Similarly, Connolly et al. (2002) observe no effect of acoustic tags on the leafy seadragon (*Phycodurus eques*) and suggest that attachment of the tags to bony appendages does not

affect behaviour. It may be that the streamer tags or the release from the boat, and not the acoustic tags, elicited the stress response observed here. The heightened movement lasted less than two days and resulted in small net displacements (less than 2/3 km), relative to the displacements observed in mark-recapture studies (e.g. Chapter 3, median displacement=8.69 km). The combination of a flight response and the low activity of lobster may have contributed to the low recapture rate of marked lobster in the study area in an experimental trap survey conducted the following year (Chapter 2).

The factors that determine activity patters may depend on the currents and light penetration. Generally, lobster are thought to be nocturnal, but a few studies have shown lobster to be more active at slack tide (reviewed by Lawton and Lavalli 1995). A comparison of step lengths during the night and day did not detect differences in movement behaviour (Fig. 4.11). Unfortunately, it is not possible to assess the activity pattern with respect to tidal regime because the movement of the hydrophone buoys, which is large relative to the movement of these lobster, results from tide and wind induced currents (Fig. 4.5). After the first day at large, the three lobster that remained in the array showed very limited movement. The tracks varied from day to day and between lobster. No single lobster was consistently the most mobile on all days, but the male (LT 3966) possessed the largest home range and had the longest step lengths.

The buoy array encompassed a sandstone ridge in an otherwise apparently flat sandy area (Don LeBlanc, lobster fishermen, Robichaud, NB; personal observation). In this area, lobster may be limited to small patches of suitable habitat. It is also possible that in the first three weeks of July, possibly in preparation for and/or during moulting or ecdysis, lobster have a very limited home range. None of the acoustic tags was recaptured

during the fishery (August-October), suggesting that all or most of the lobster tagged for this study moulted, died or otherwise lost their tags. I expect that the mortality rate of the tagged lobster was high because the attachment of the acoustic tags spanned the mid-dorsal line which opens during ecdysis.

The very restricted movement or activity of the resident, or possibly just overwintering, lobster in the month of July may account for the low catchability of lobster in the Northumberland Strait in the spring (Chapter 2). Furthermore, a positive correlation between movement behaviour and catchability may contribute to the high mobility documented by mark/recapture tagging studies. And, if resident lobster are associated with complex habitat such as a sandstone ridges, which are purposefully under-sampled by the trawl survey, the less-mobile resident lobster would be under-represented in the trawl caught lobster, which comprised the majority of the lobster tagged for the mark/recapture tagging study (Chapter 2).

This first-time use of RAPT in the Northumberland Strait indicates the potential for this method to track small-scale lobster movement in this area, despite the bias produced by the movement of the hydrophone array (Fig. 4.6). Using data from a RAPT buoy array of similar dimension, Tremblay et al. (2003) estimated that the radial component of the error to be less than 2 m in the center of array, which is comparable to the present study. Future RAPT deployments to study lobster activity and habitat use in this area could improve the accuracy of the system by reducing the distance between the hydrophones. In addition, the accuracy of the system could be improved by obtaining more data on, or a model of, the hydrophone buoy positions before triangulating acoustic

tag positions, or by fixing the hydrophone positions. For example, the hydrophones could be anchored closer to the bottom (e.g. Bradbury et al. 1995).

Many underwater telemetry systems have been developed using lobster as test animals (Lund 1970, Jernakoff 1987, Smith et al. 1998, O'Dor and Webber 1991), despite the range in movement patterns within and between individuals (Lund et al. 1973, Herrnkind 1980, Ennis 1984, Phillips et al. 1984, Karnofsky et al. 1989a, 1989b). The very limited movement of the resident lobster of the central part of the Northumberland Strait in the early summer may make these lobster an ideal study organism for the RAPT system.

Table 4.1. Summary of the VEMCO VR16 radio acoustic tags attached to four female lobster, two male lobster and two traps. Market-size lobster ($\geq$ 81 mm CL) were caught and kept in traps up to four days prior to release on July 1, 2001. The lobster can be identified by the color indicated in the plots of lobster tracks.

VR60 Tag Number	Frequency KHz	Date of Capture	Carapace Length mm	Color
Female lobster				
LT 3964	57	June 27 or July 1	81 or 95	Gray
LT 3965	60	June 27 or July 1	81 or 95	Red
LT 3967	66	June 27	82	Blue
LT 3968	72	July 1	88	Aquamarine
LT 3969	75	June 26	95	Brown
LT 3970	78	July 1	85	Yellow
Male lobster				
LT 3962	51	June 26	114	Navy
LT 3966	66	June 26	93	Green
Trap / Fixed				
TT 3963	54	-	-	Black
TT 3812	69	-	-	Black

Table 4.2. Summary of the position data collected using RAPT and a mobile hydrophone. The triangulated positions were filtered to remove echoes and merged with the position data for the reference trap (TT 3812). The number of days for which data is available after filtering and merging is indicated.

VR16 Tag Number	Day in July on which tags were positions by mobile hydrophone	Number of positions / number of days	Number of positions / number of days, after filter	Number of positions / number of days, after filter and merge
Female lobster				
LT 3964	4, 7, 9, 18	296 / 17	244 / 16	-
LT 3965	-	4987 / 29	4270 / 29	3807 / 28
LT 3967	-	5170 / 29	4465 / 29	3958 / 28
LT 3968	5, 7, 9, 18	11/ 2	10 / 1	-
LT 3969	4, 9	15 / 1	13 / 1	-
LT 3970	5, 7, 9, 18	1894 / 29	951 / 28	-
Male lobster				
LT 3962	5, 7, 18	256 / 8	228 / 7	-
LT 3966	-	3417 / 25	2800 / 24	2561 / 23
Trap / Fixed				
TT 3963	-	5275 / 29	4701 / 29	4174 / 28
TT 3812	-	5274 / 29	4750 / 29	-

Table 4.3. Summary statistics from the correlation analysis to correct positions for movement of the hydrophone array. For each time period (days decimal), the degrees of freedom (df) and the correlation coefficient (adjusted r-squared) between the displacement (m) in the x and y directions between the one reference tag attached to a trap and four focal tags. One focal tag was attached to a trap, and the 3 other focal tags were attached to lobster.

Time Period	Trap TT 3963	Lobster 1 LT 3965	Lobster 2 LT 3966	Lobster 3 LT 3967
182.863 to 184.669				
df	63	58	26	67
x-direction r-squared	0.9329	0.7215	0.8998	0.8919
y-direction r-squared	0.9496	0.7231	0.2308	0.7101
184.711 to 185.600				
df	227	192	64	227
x-direction r-squared	0.9681	0.8672	0.8060	0.9662
y-direction r-squared	0.9515	0.7867	0.0074	0.9049
185.683 to 186.542				
df	152	146	116	153
x-direction r-squared	0.9539	0.9703	0.7808	0.9809
y-direction r-squared	0.9599	0.9685	0.6176	0.9692
186.584 to 188.584				
df	263	219	193	275
x-direction r-squared	0.9633	0.9263	0.9374	0.9582
y-direction r-squared	0.8906	0.6431	0.4836	0.5757
188.626 to 190.389				
df	308	249	201	266
x-direction r-squared	0.9855	0.8392	0.9483	0.7800
y-direction r-squared	0.9598	0.3416	0.6961	0.4583
190.473 to 192.392				
df	330	298	294	330
x-direction r-squared	0.9730	0.8934	0.8245	0.9563
y-direction r-squared	0.9418	0.6089	0.7851	0.8887
192.434 to 194.434				

df	343	323	296	327
x-direction r-squared	0.9828	0.9662	0.8147	0.9243
y-direction r-squared	0.9797	0.8855	0.6516	0.8791

194.475 to 195.430

df	165	151	99	151
x-direction r-squared	0.9857	0.8605	0.7936	0.6391
y-direction r-squared	0.9755	0.7880	0.6483	0.6247

195.472 to 197.400

df	342	319	286	325
x-direction r-squared	0.9709	0.9563	0.8704	0.8770
y-direction r-squared	0.9743	0.9025	0.8524	0.9132

197.442 to 199.481

df	290	285	240	295
x-direction r-squared	0.9809	0.9590	0.8650	0.9483
y-direction r-squared	0.9252	0.7797	0.7083	0.4914

199.523 to 201.724

df	363	344	306	346
x-direction r-squared	0.9849	0.9749	0.9333	0.9785
y-direction r-squared	0.9666	0.7257	0.8807	0.9375

201.766 to 207.644

df	903	843	416	845
x position r-squared	0.9829	0.9406	0.7728	0.7129
y position r-squared	0.9331	0.9040	0.5562	0.4778

207.686 to 210.552

df	399	354	-	325
x position r-squared	0.9805	0.9267	-	0.8653
Y position r-squared	0.9471	0.8545	-	0.7528

Table 4.4. Summary of focal trap and lobster movement. The days for which the focal lobster were the farthest from their own center of activity, 95% confidence interval of the x- and y- displacement, and the median step lengths and time of steps.

Tag Number	Days which the lobster was farthest from center of activity	Confidence interval for x-displacement from center of activity, m	Confidence interval for y-displacement from center of activity, m	Minimum Convex Polygon of 100% of positions, m²	Minimum Convex Polygon of 95% of positions, m²	Minimum Convex Polygon of 50% of positions, m²	Median step length, m	Median time of step, min
Focal trap								
LT 3962	-	1.1243	0.8649	75.02	10.35	1.59	0.6311	6.4368
Focal lobster								
LT 3965	2, 6, 7, 9, 10, 27	3.6862	4.0341	240.39	49.53	4.43	1.0429	6.4512
LT 3966	3-5, 11, 12, 14-21, 23, 24	8.1754	6.7320	564.77	75.00	7.95	1.4797	6.4800
LT 3967	8, 13, 22, 25, 26, 28, 29	8.2717	6.3254	1501.31	59.94	5.30	0.9949	6.4368
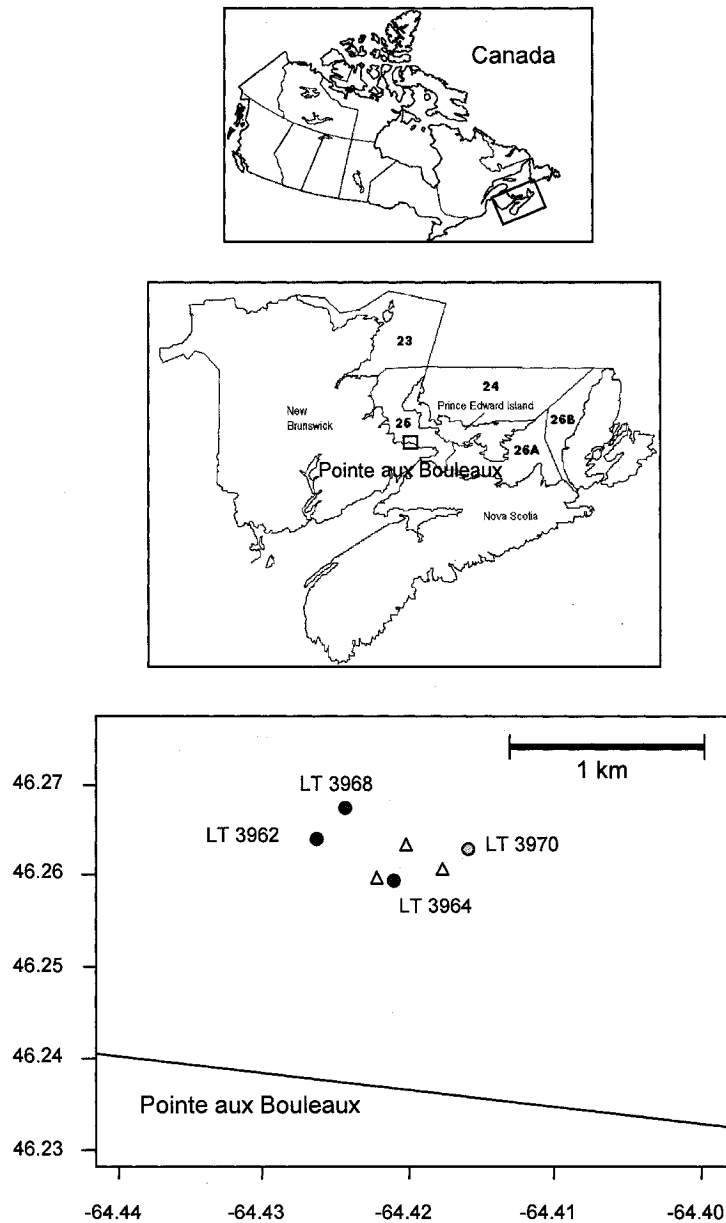
Fig. 4.1. Maps of Canada (A), the maritime provinces (B), and the positions of the hydrophone buoys and the lobster that moved outside of the hydrophone array (C). The VEMCO RAPT triangular array of hydrophone buoys was deployed in 7-12 m (25-35 ft) deep water off of Pointe aux Bouleaux, New Brunswick. The triangles indicate the position of the hydrophone buoys. Of the eight lobster released with telemetry tags, three stayed within the array, and four were positioned using mobile hydrophones just outside of the array. The positions of the four lobster located on July 18, 2002, the final day of searching with the mobile hydrophone are plotted and the tag numbers indicated.

Transmitter Attachment

Transmitter Attachment Detail

Profile View

Rubber Mount

Plan View

Transmitter
(secured to rubber mount with epoxy)

Monofilament Line
(secured to transmitter with epoxy)

Rubber Mount
(underside secured to lobster
carapace with epoxy)

Cross Section View

Transmitter

Rubber Mount
Lobster Carapace

Transmitter Detail

Battery

Transmitter

Battery terminal wires
soldered to leads on transmitter

Fig. 4.2. Diagram of acoustic tag attachment to lobster. Acoustic tags were attached to lobster using epoxy. The rubber foot provided a larger surface area for attachment (Diagrams by Ken Bryenton).

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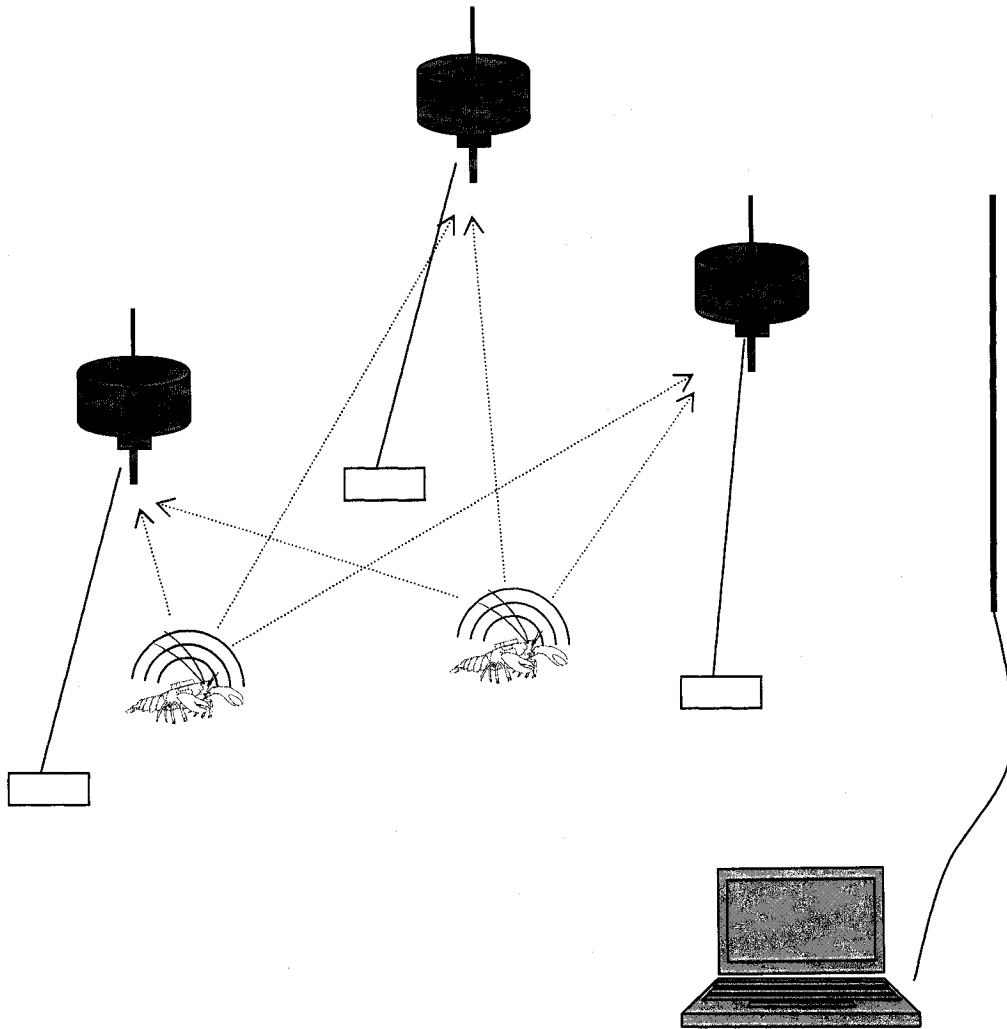
Fig. 4.3. Diagram of the VEMCO RAPT system including hydrophones with radio transmitters and the base station, which records the time at which signals are received by three hydrophones (raw data) and triangulates the positions of telemetry tags.
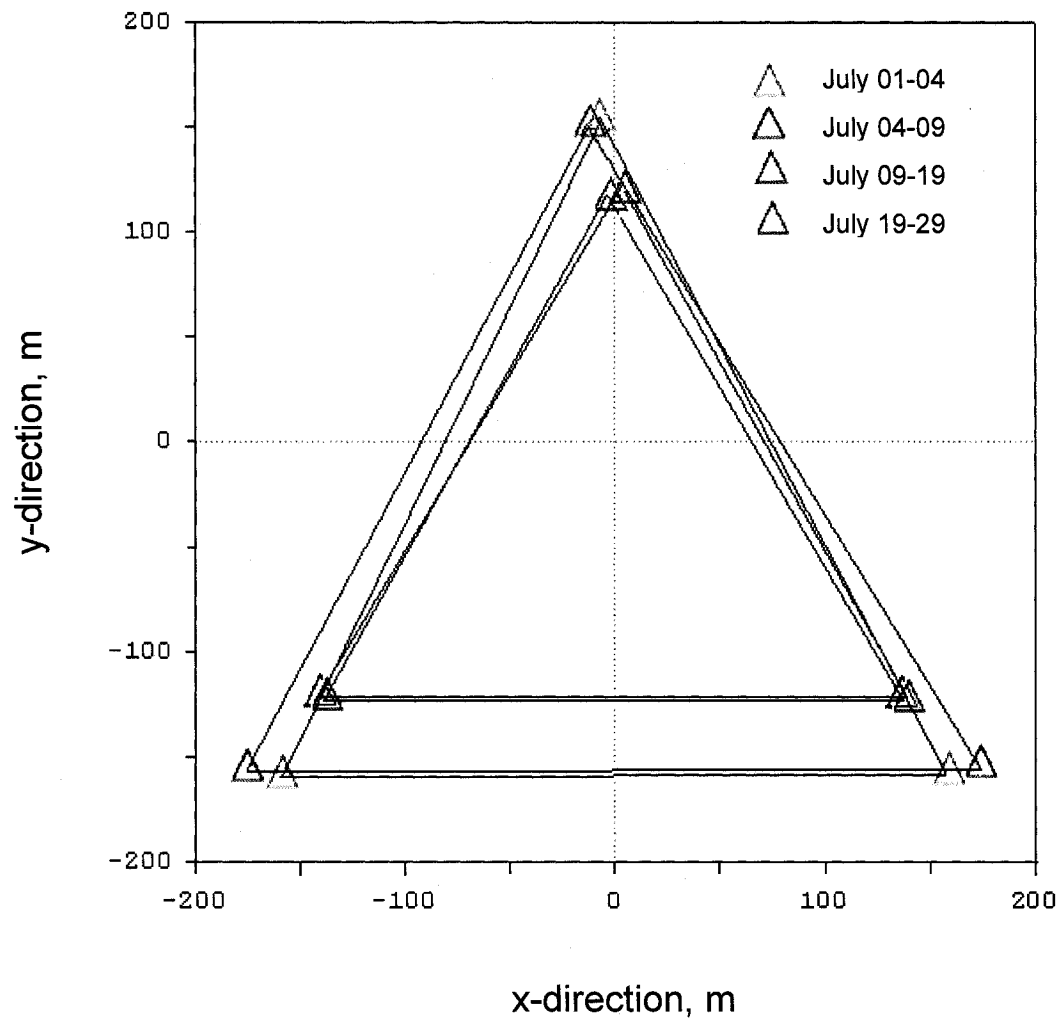
Fig. 4.4. Mean position of hydrophone buoys for four time periods used in post-analysis.
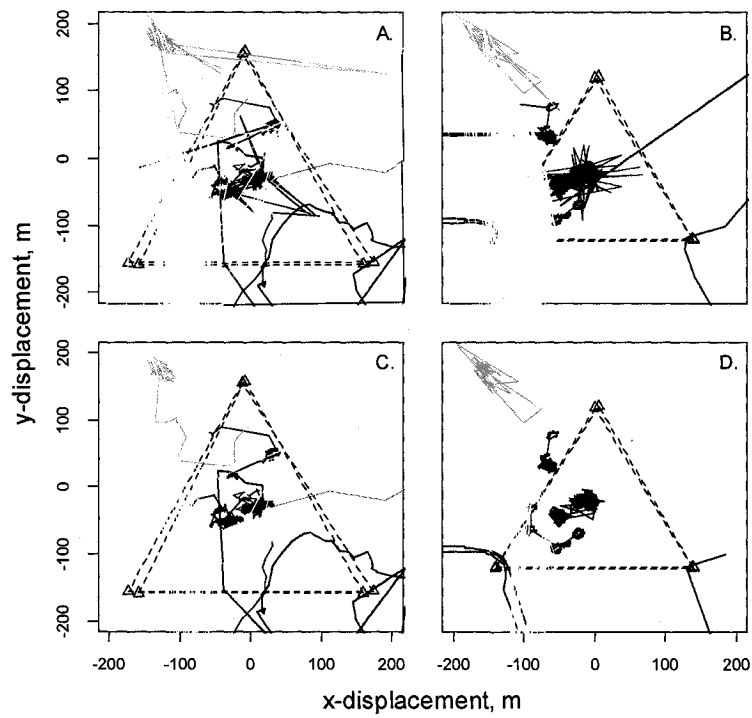
Fig. 4.5. Plots of unfiltered (A) and filtered positions (C) triangulated from the hydrophone array assuming fixed positions for the hydrophone buoys prior to July 9, 2001 (time periods 1 and 2). Plots of the unfiltered (B) and filtered (D) positions after July 9, 2001 (time periods 3 and 4). The hydrophone buoy array is overlayed (open triangle and dashed lines). Female Lobster: LT 3964 Gray; LT 3965 Red; LT 3967 Blue; LT 3968 Aquamarine; LT 3969 Brown; LT 3970 Yellow. Male lobster: LT 3962 Navy; LT 3966 Green. Trap: TT 3812 Black.
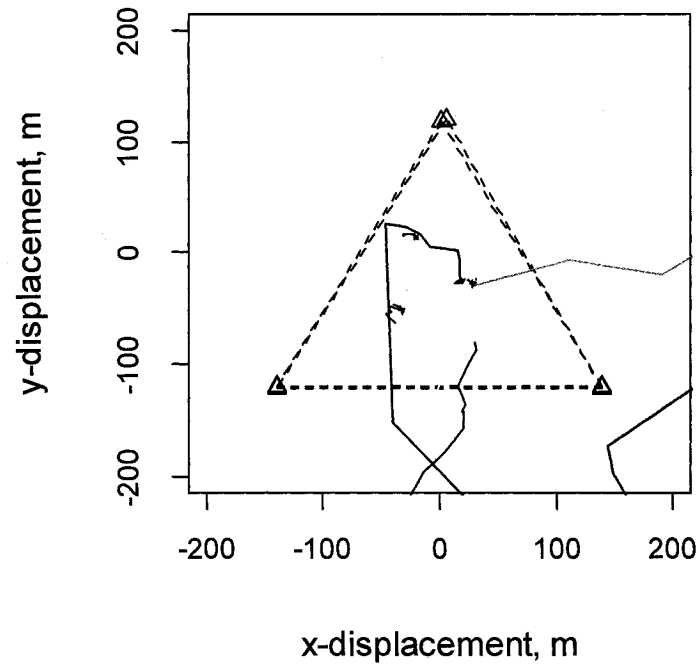
Fig. 4.6. Filtered, but not corrected, lobster tracks between release and midnight of July 1, 2001. The black track is the perceived movement of a trap. The hydrophone buoy array is overlayed (open triangle and dashed lines). There are no data available during this time period for one lobster (LT 3964) and the one trap (TT 3963).
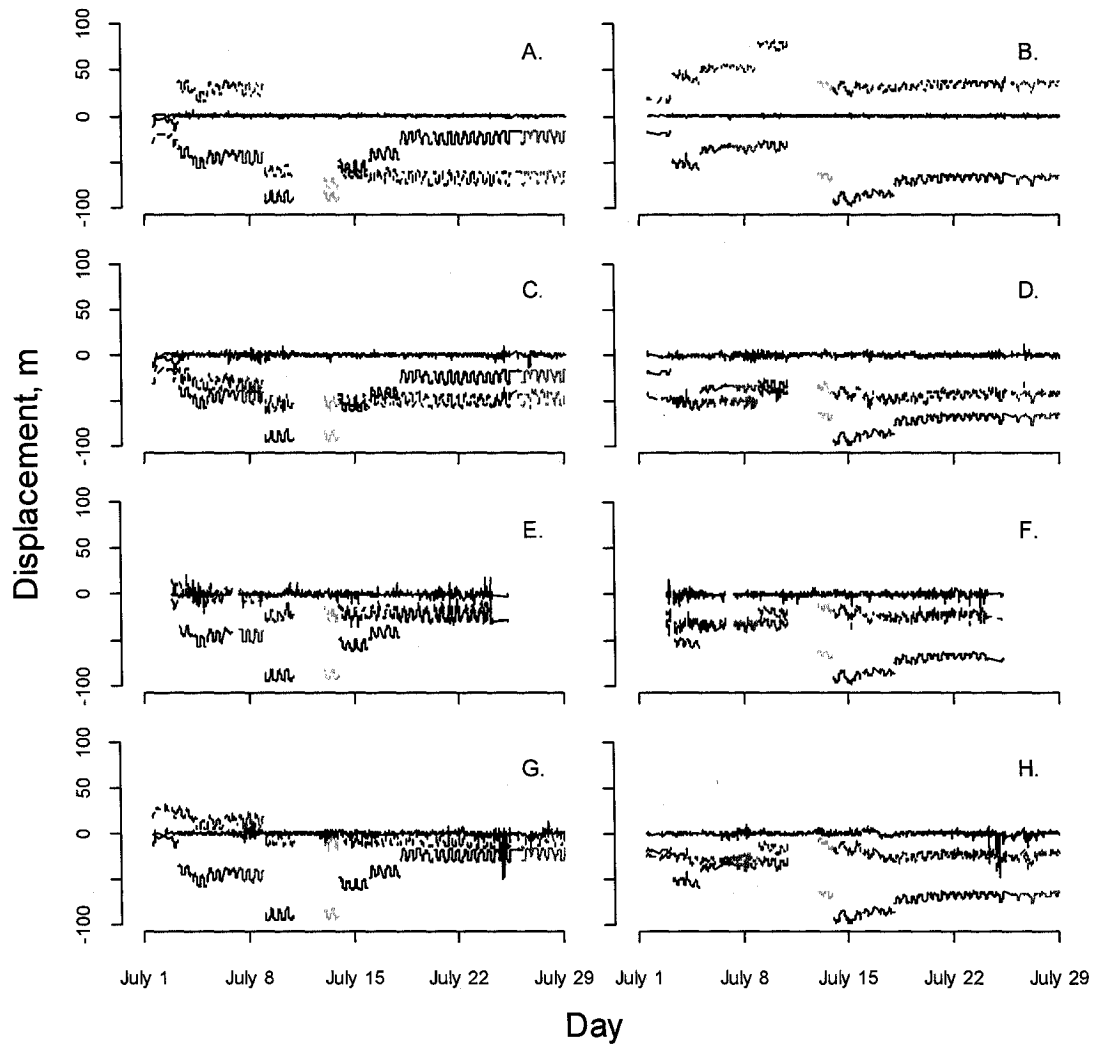
Fig. 4.7. Plots of the corrected displacements in the x- (A) and y-direction (B) of the reference tag (solid line) and the focal tag attached to the trap (dashed line). Plots C and D are the displacements in the x and y-direction of lobster LT 3965, plots E and F are the displacement of lobster LT 3966 and plots G and H are lobster LT 3967. There were thirteen time periods represented by different colors in which the reference tag is in a fixed position relative to the focal tag. The solid black line is the plot of residuals of the focal tag position predicted by the reference tag.

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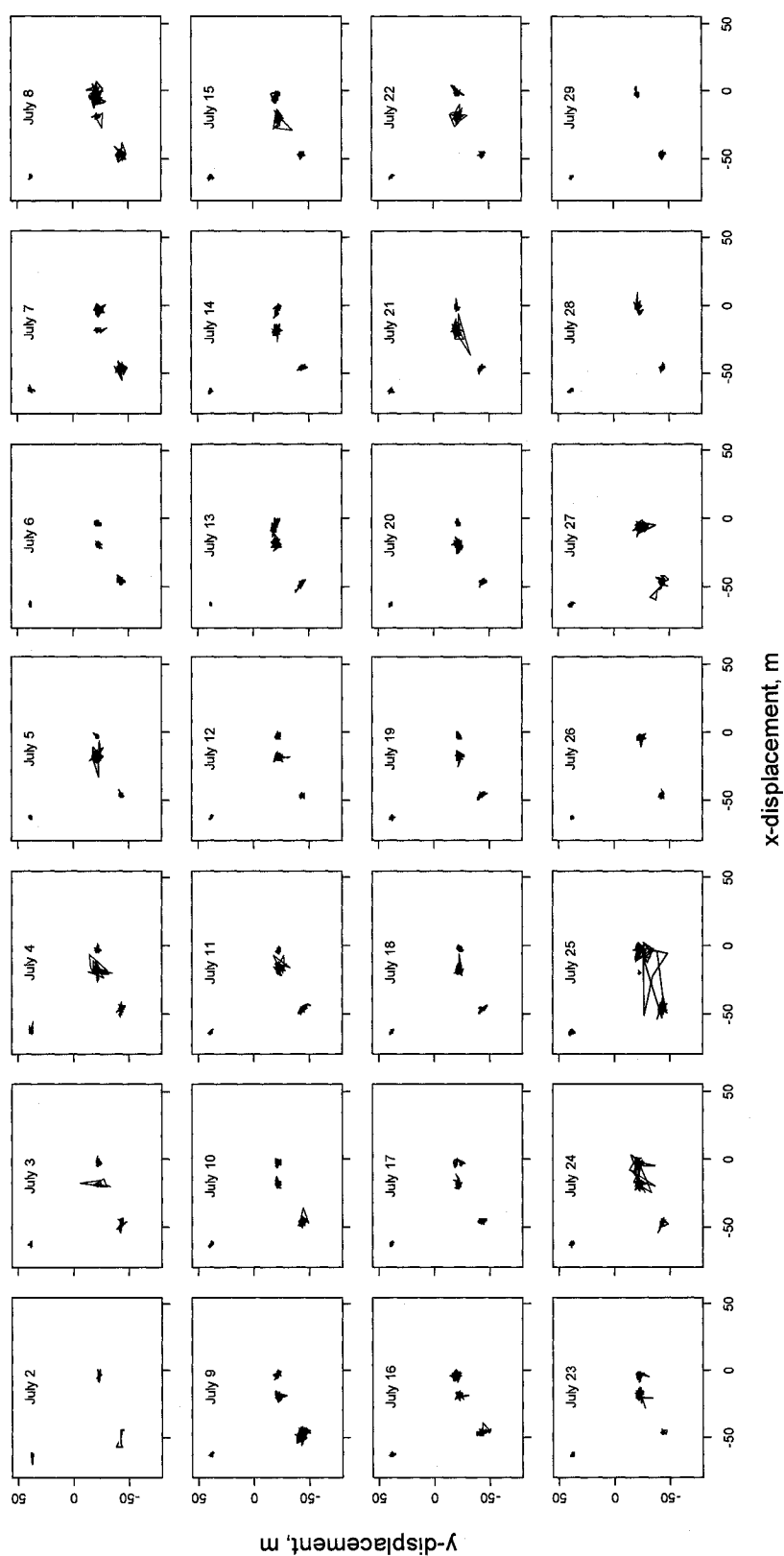
Fig. 4.8. Plots of the corrected positions per day for focal trap and three lobster that remained inside the hydrophone array. Trap TT 3963 – Black, Lobster LT 3965 - red, Lobster LT 3966 - green, Lobster LT 3967 -blue.
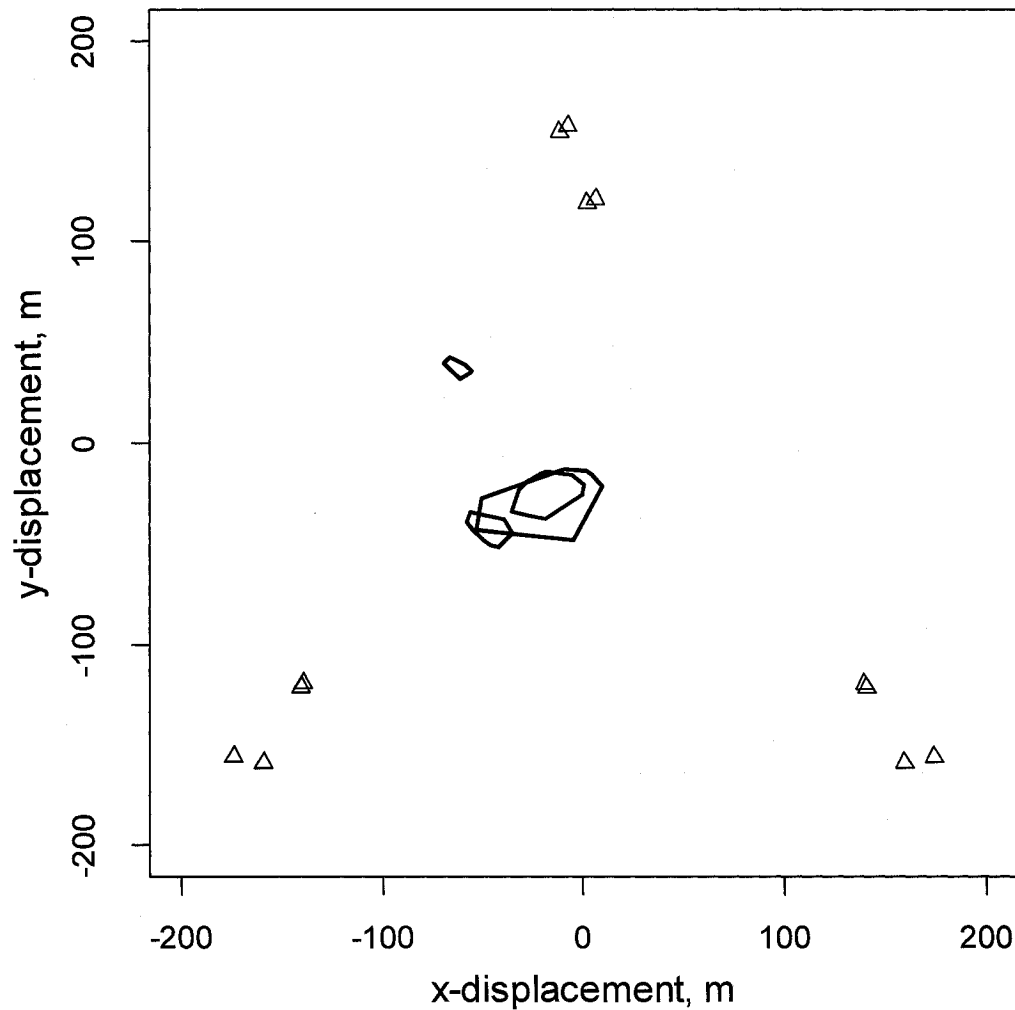
Fig. 4.9. Plots of the Minimum Convex Polygons (MCPs) that describe the corrected positions of the focal trap and lobster. Trap – Black, Lobster LT 3965 - red , Lobster LT 3966 - green, Lobster LT 3967 -blue. The triangles indicate the hydrophone buoy positions.
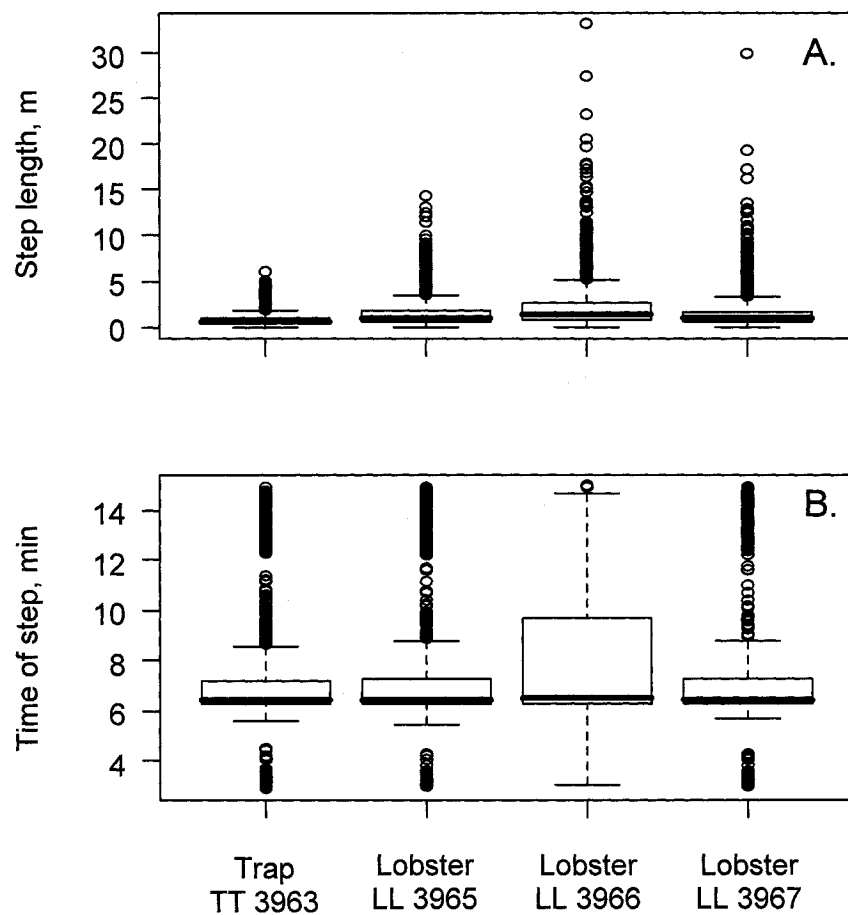
Fig. 4.10. Boxplots of step lengths (A) and time of steps (B) of less than 20 minutes for the focal trap and lobster. One step length of 79.64 m for lobster LT 3965 is not plotted.
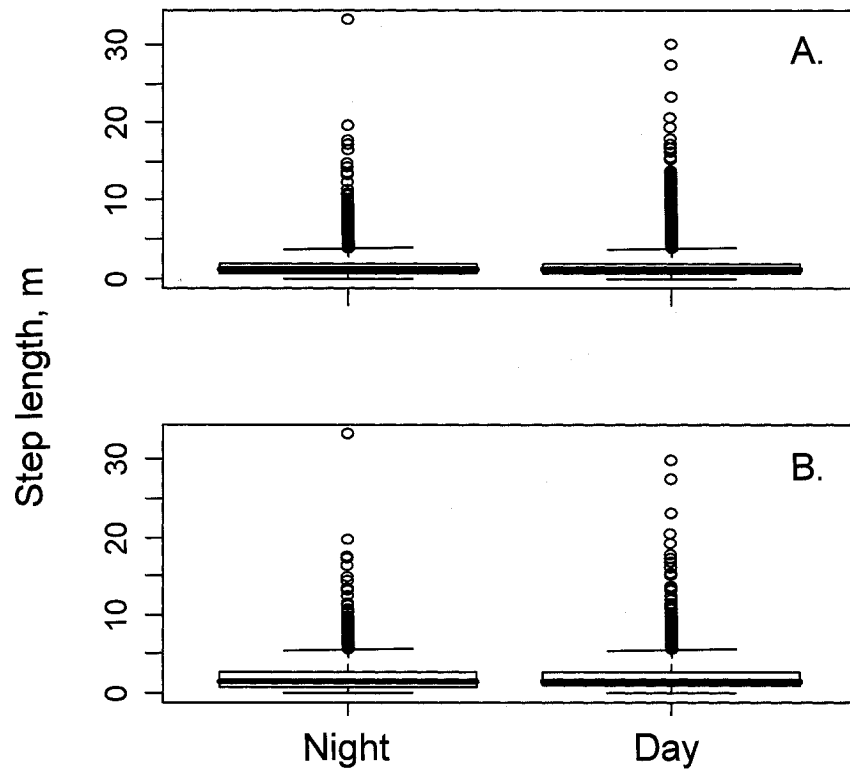
Fig. 4.11. Boxplots of step lengths of less than 20 minutes in the day and night for all the lobster (A) and for only the most active lobster of each day (B). One step length of 79.64 m at night is not plotted.

CHAPTER 5

Conclusion

Understanding the patterns and mechanisms of movement is critical to the management of exploited populations. The American lobster (*Homarus americanus*) fishery is one of the most economically and socially important fisheries on the Atlantic coast of North America. While it is widely recognized that adult lobster are highly mobile, relatively little is known about population structure. The primary focus of this work was to study the movement of lobster in the Northumberland Strait, specifically to answer the question of whether lobster migrate into lobster fishing area (LFA) 25. In the work presented here, I used both Lagrangian and Eulerian, and fishery-dependent and fishery-independent, methods to document changes in lobster distribution in a shallow strait, and track individual lobster movement over small and large temporal and spatial scales.

Eulerian methods monitoring changes in the distribution of a population, such as experimental traps (Jeffries and Johnson 1974, Bergeron 1967, Munro and Therriault 1983, Moriyasu et al. 1998, Howell et al. 1999, Chapter 2) and direct observation of abundance by SCUBA diving and snorkeling (Ennis 1984, Karnofsky et al. 1989a, 1989b) have provided the most robust evidence to date for seasonal inshore/offshore lobster migration. In Chapter 2, I present the results of experimental trawl and trap surveys that show the immigration of lobster into the central part of the Northumberland Strait in July, 2001. A change-in-ratio analysis of the trap catches and the trawl survey suggest that the over-wintering population tripled. A similar pattern in trap catches in Shediac Bay in July 1932 and Egmont Bay in 1981, and the observations of the local fishermen, suggest that this phenomenon has occurred historically, if not annually.

The immigration or mass movement of lobster into the Northumberland Strait could result from migration or dispersal. Immigration could be half of a seasonal inshore/offshore migration that makes use of the shallow warm waters of the Northumberland Strait during the summer. Immigration could also result from an ontogenetic habitat shift or dispersal from larval settlement areas or over-wintering habitat. This may or may not result from density-dependent dispersal.

In Chapter 3, I use a Lagrangian approach and a large-scale opportunistic mark/recapture study to track individual lobster movement. I found no evidence for directed movement into the Northumberland Strait. Unfortunately, very few lobster were tagged in October, May and June, when both abundance and catchability are low. While the sequential increase in catch in lobster traps from northwest to the southeast along the axis of the strait, confirms the observation of fishermen, and suggests a mass movement or migration into the strait, there is no directional bias to the movement of individual lobster released in July and August and recaught during the fishery. The lack of directional bias is consistent with previous studies (Templeman 1936, Wilder 1963, Comeau and Savoie 2002). Indeed, as Templeman (1936) observed:

> "The results from both areas show no definite migration but a wandering
> with resulting scattering, the lobster population on the whole remaining
> more or less local in character."

Lobster released in areas of high lobster density move less than those at low density, suggesting that the observed diffusion is either part of an ontogenetic shift or dispersal behaviour. Density-independent diffusive or dispersal movements and a density gradient could explain the observed pattern of population movement and the directionally unbiased movement of individual lobster. A similar pattern and mechanism of movement

was hypothesized for lobster inhabiting the waters around the Magdalen Islands, as noted by Montreuil (1960):

> "Returns from extensive tagging over a period of several years showed no true migratory pattern. ... Magdelen Islands lobster is nurtured mostly on the South side...as it grows and matures, it scatters...This would explain the continued relative lack of small lobster on the latter [North-side grounds]."

The increase in the diffusion coefficient with time-at-large suggests that individual movement is directionally persistent and best described by a correlated random walk model.

With the individual mark/recapture data I also test hypothesis of sex- and size-biased movement. Male-, female- and ovigerous-female-biased movement has been documented in various tagging studies. I document female-biased movement in the Northumberland Strait during July and August and argue that this bias is consistent with female mate/den searching behaviour. Further the slightly greater propensity of male lobster to home to the direction of initial capture may also be linked to male territorial behaviour associated with mating and moutling. In estuaries male-biased movement may result from greater physiological tolerance and hence more available habitat (Jury et al. 1994a, 1994b). I suggest that diffusion models could be used to test hypotheses on the physiogeographic and behavioural determination of movement in lobster.

As with most opportunistic tagging studies that rely on reports from commercial fisheries, the recaptured lobster were predominantly at or just above the minimum legal size (55-122 mm CL), which may have precluded the detection of size-biased and or maturity-biased movement. Fishery-independent research on the movement behaviour of

juvenile and smaller lobster could contribute to a better understanding of movement behaviour and patterns.

Research on lobster population structure also requires an understanding of larval dispersal. Long-distance movement of adult lobster could contribute to the lifetime displacement, but without a better understanding of larval ecology, distribution and settlement patterns, it is not possible to make inferences about lobster population structure. Further, opportunistic mark/recapture studies are biased by fishing or observation effort, but the modeling and statistical analyses that have been developed to overcome this bias have not been employed, possibly because, as with the present research, translation of individual movements into population redistribution would require an assessment of the initial population distribution, which is conspicuously absent in most areas.

> "…Absent from most resource (American lobster) assessments is detailed information on spatial and temporal patterns of abundance. In stark contrast, ecological approaches typically begin by quantifying patterns of distribution and abundance." (Steneck and Wilson 2001)

In Chapter 4, I used radio-acoustic positioning and telemetry (RAPT) to track the small-scale movement of lobster in the central part of the Northumberland Strait. While the sample size in my RAPT pilot project is very limited, this work showed that the home ranges of resident or over-wintering lobster in the central part of the Northumberland Strait in July were limited and there was no difference in activity during night and day. It is not possible to assess whether the individual lobster tagged in this study would have maintained this distinct residential or station-keeping behaviour or would have changed behaviour, perhaps after moulting and mating. Previous studies have suggested that

lobster alternate between homing or station-keeping behaviour and nomadic or ranging movement (Ennis 1984, Watson et al. 1999). For example, in a shallow New England bay an alternation between two to three weeks of station-keeping or resident behaviour and short bursts of directionally persistent movement has been tracked using acoustic tags and a mobile hydrophone (Watson et all 1999). Notably, seven of the eight lobster tagged moved less than 2/3 of a km, which is small compared to the movement observed in mark/recapture tagging studies in the same area (Comeau and Savoie 2002, Chapter 3).

Lobster have been used as a model organisms for electromagnetic and acoustic telemetry (Lund 1970, Jernakoff 1987, Smith et al. 1998, O'Dor and Webber 1991), despite the fact that the capacity and variety of lobster movement behaviour is beyond the scope of small-scale telemetry arrays. However, the lobster in the central part of the Northumberland Strait during July exhibit very limited home range, which is ideal for study with a fixed acoustic array. With improvements in the VEMCO RAPT system to reduce bias associated with the movement of the hydrophone buoys, the RAPT system could be used to study the small-scale movement behaviour of the resident or over-wintering lobster in this area. Such research would be complemented by using a mobile hydrophone or additional fixed hydrophones over larger temporal and spatial scales to better assess whether the heterogeneity in lobster movement results from plasticity or heterogeneity among individuals.

The study of animal movement demands careful consideration of spatial and temporal scales; this is particularly true for lobster, which possess considerable within- and among-individual variability in movement behaviour (Herrnkind 1980, Ennis 1984, Watson et al. 1999). The source of movement heterogeneity, whether it is among

populations or sub-populations, within populations or within individuals, is fundamental to conservation and management.

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